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THE

BOTANICAL GAZETTE

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JOHN MERLE COULTER

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WITH THIRTY-EIGHT PLATES AND ONE HUNDRED AND FIFTEEN FIGURES

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ERRATA

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P. 28, line 10 from bottom, for *Seemanii* read *Seemannii*

P. 36, line 11 from top, for eaves read leaves

P. 39, line 18 from top, for antithesis read anthesis

P. 377, line 5 from bottom, for Populis-Salix read Populus-Salix

P. 428, line 12 from top, for my read the

VOLUME LXIV NUMBER 1

THE
BOTANICAL GAZETTE

JULY 1917

THE ARCHEGONIUM OF CATHARINEA ANGUSTATA BRID. (ATRICHUM ANGUSTATUM)

GEORGE S. BRYAN

(WITH PLATES I–VIII AND ONE FIGURE)

The archegonium of the Musci has been studied by numerous investigators, but the accounts of the developmental processes, especially the development and growth of the canal row, are so varied and even contradictory that the whole subject is in need of reinvestigation. *Catharinea* has been selected for an initial study because it is a representative of the most advanced group of the Musci. The results of studies of representatives of lower groups will appear later.

Material and methods

Catharinea is quite abundant in the region about Madison. The particular species here studied is *Catharinea angustata* Brid., as identified by Mrs. ELIZABETH G. BRITTON, to whom the author is greatly indebted for this courtesy. This entire investigation has been made on what is probably dioecious material. The sex organs were found not only on different gametophores, but these upright branches occur in relatively large, well defined patches or clusters of one sex or the other. A few cases were found in which the patch contained the upright branches of both sexes mixed together indiscriminately. The evidence here presented, while suggestive, is not conclusive of dioeciousness. An exact determination must await careful experimental work from spore to mature

plants. Abundant monoecious material, identified by Mrs. BRITTON as belonging to the same species, has been found at other stations, but this has been reserved for a later investigation.

Like many of the Musci, *Catharinea* displays evidence of being quite plastic. Thus plants taken from the same patch have shown striking variations in the number of lamellae; and even on different leaves of the same plant the number of lamellae may fluctuate beyond the limits given in taxonomic descriptions. The writer has little sympathy with the present tendency toward the manufacture of endless numbers of species on extremely slender bases. In regard to *Catharinea* careful investigations are needed to determine whether these minor differences are in reality specific, or are merely the fluctuations of a plastic form.

C. angustata forms archegonia rather early in the spring. Frequent collections were made at Eagle Heights, about 4 miles from the city, beginning the first week in April and ending the latter part of May. This was supplemented by other collections from stations on the campus and from Dorwood's Glen. The plants were transferred to large moist glass jars and almost daily killings made, thus securing a wealth of material for study. The killing agents used were 0.25 chrom-acetic and Flemming's medium. For the study of young stages serial paraffin ribbons were cut 5–6 μ; for the older stages 8–12 μ. As stains, safranin in combination with Licht Grün, Flemming's triple, and Heidenhain's iron alum hematoxylin were employed.

In staining moss material 10 μ or more in thickness the difficulty is often experienced that during the process some of the sections are almost certain to wash off, especially in the iron alum hematoxylin combination. This trouble was avoided through the use of a modification of the fixative devised by LAND (11). By experimentation the least possible amounts of gum arabic and chromic acid effective in 100 cc. of water were determined. Through the use of this there was no discoloration of the sections and staining was not interfered with. It was also found that standing the slides on end and allowing the excess fixative to drain off aids in preventing discoloration. CHAMBERLAIN (3, p. 114) states that this fixative will not keep. The writer, remembering a sug-

gestion once offered by LAND, has, in a well blackened bottle, fixative nearly a year old which is just as efficient as when first made up.

Historical

HOFMEISTER (6) in 1851 published the first account of the developmental processes in the archegonia of the Bryophyta. He examined a number of forms both among the Hepaticae and the Musci. In the latter group he found the antheridium and the archegonium exactly alike in the early stages of development, a fact which has been confirmed by subsequent investigations; but his account of the formation of the archegonium proper has received no confirmation from later workers. It is of interest therefore only from a historical standpoint. Among the Musci HOFMEISTER seems to have examined *Sphagnum*, *Phascum*, *Archidium*, *Funaria*, *Fissidens*, *Dicranum*, and *Polytrichum*.

In the early stages the growth is by an apical cell with two cutting faces. In each of the 2 cells thus formed there occurs a radial longitudinal division. The young archegonium now consists of 4 rows of cells. Then the formation of the archegonium proper takes place. In this process the cells of one of these longitudinal rows divide parallel to the outer wall, thus producing a central row of cells (the canal row) surrounded by 4 peripheral cell rows. Later 2 of these peripheral cells divide, thus completing the 6 cells of the periphery of the neck.

In 1858 SCHIMPER (12) published his historic monograph on *Sphagnum*. He describes the early stages in archegonial development as arising through the activity of an apical cell with 2 cutting faces, thus confirming the account given by HOFMEISTER. He is unwilling to commit himself in regard to the origin of the archegonium proper, however, referring the reader to HOFMEISTER'S account in the mosses, which he is able neither to affirm nor to deny.

KÜHN'S (10) interpretation of the development of *Andreaea* appeared in 1870. His account of the origin of the archegonium proper differs radically from that given by HOFMEISTER. He found that in the uppermost cell, which finally becomes the mother cell of the archegonium proper, 3 walls appear in such a way as to cut

out 3 peripheral segments and originate a central cell. The central cell now divides into an outer and an inner cell. The latter is the first cell of the axial row. The outer cell grows considerably, and again the 3 peripheral segments and the inner cell are cut off. The latter divides into an inner and an outer cell. Thus the second cell of the axial row arises just as did the first, and KÜHN holds that all subsequent cells of the axial row are produced in the same manner.

In 1872 JANCZEWSKI (9) made a study of the archegonia of several mosses. He names 2 species of *Sphagnum*, *Atrichum* (*Catharinea*) *undulatum*, *Bryum crudum*, *Funaria hygrometrica*, and *Phascum cuspidatum*. JANCZEWSKI'S account of the development of these mosses is very brief. He mentions only the chief points, and gives no details. It is unfortunate also that the paper has no illustrations. In regard to *Atrichum undulatum*, *Bryum crudum*, *Funaria hygrometrica*, and *Phascum cuspidatum*, his chief points are as follows: There is development by an apical cell with 2 cutting faces, producing a few-celled structure which at this time cannot be distinguished from a young antheridium. In the uppermost cell, which is to be the mother cell of the archegonium proper, there now appear, just as KÜHN described for *Andreaea*, 3 oblique walls cutting off 3 peripheral segments and forming a funnel-shaped inner cell. This inner cell then divides to form an outer cell (the cover cell) and an inner cell. This last formed inner cell again divides, the lower cell being the ventral cell of the archegonium, while the upper cell is the primary neck canal cell. The cover cell continues to act as an apical cell, cutting off peripheral segments and canal initials. The number of canal initials varies from 2 to 6. The cover cell may cut off 1, 2, or 3 peripheral segments before forming a new canal initial. That is to say, there is no mathematical proportion between the cutting off of peripheral segments and canal initials. In the growth of the canal row the cells are of different origins. The upper cells arise through the cross divisions of the 2–6 canal initials, while the lower cells arise through the transverse divisions of the primary canal initial. The archegonium of *Sphagnum* is reported in general to show the same sort of development that has been described for the other mosses.

In 1884 Hy (8) summarized the archegonial situation in the Musci as well as in other groups. His paper is noteworthy only for its philosophical considerations. In a very general way he confirms the findings of Janczewski, but adds little that is new or convincing to the subject.

In 1895 Campbell (2, pp. 201, 202) studied the development of the archegonium of *Funaria hygrometrica*. Here the first division separates a basal cell from a terminal cell, which is the mother cell of the archegonium proper. "In the latter 3 walls now arise, as in the Hepaticae and *Andreaea*, but in *Funaria* they do not all reach the basal wall, but intersect at some distance above it, so that they inclose a tetrahedral cell, pointed below instead of truncate." The tetrahedral cell makes the usual division into "cover cell" and inner cell. The latter now divides, forming the primary neck canal cell and the ventral cell. "The cover cell instead of dividing by quadrant walls has a regular series of segments cut off from it and acts as an apical cell. These segments are cut off parallel both to its lateral faces and base and thus form 4 rows of segments, the 3 derived from the lateral faces forming the outer neck cells, and the row of segments cut off from the base constituting the axial row of neck canal cells." As to the further growth of the canal row, Campbell states that the canal cells, "so far as could be determined, do not divide after they are first formed."

Gayet (4) in 1897 undertook a re-examination of the whole question of archegonial development in the Bryophyta, the investigation covering numerous forms both among the Hepaticae and the Musci. In the latter group, which alone interests us in the present discussion, he mentions 3 species of *Sphagnum*, 2 of *Andreaea*, and the following members of the Bryales: *Archidium*, *Ephemerum*, *Pleuridium*, *Phascum*, *Diphyscium*, *Barbula*, *Orthotrichum*, *Eucalyptra*, *Bryum*, *Mnium*, *Fissidens*, *Fontinalis*, and *Hypnum*. Summing up the main points of his study Gayet arrives at the following conclusions (p. 241):

1. L'archégone des Hépatiques se développe, non seulment par croissance intercalaire, mais encore par croissance terminale.

2. Chez les Mousses cette croissance terminale contribué fortement a l'allongement de l'organe femelle; il n'y a donc pas seulement 5 ou 6 segments.

3. La cellule terminale ne donne point de cellules de canal, pas plus chez les Mousses que chez les Hépatiques.

4. Les cellules de canal du col ont toutes la même origine; elles proviennent toujours d'une initale détachée de la cellule mère de l'oosphère; il n'y en a point d'adventives qui seraient formées aux dépens de la cellule terminale.

GAYET'S conclusions, therefore, are diametrically opposed to those reached by other investigators.

In 1898 GOEBEL (5) gives a rather brief and unsatisfactory account of his examination of *Mnium undulatum*. He states (p. 17): "I find in this plant confirmation throughout of the statements of JANCZEWSKI and others, and that the archegonium of the Musci is to be distinguished from that of the Hepaticae by its peculiar apical growth" (text fig. 1). The cell represented as apical in this figure is most certainly not the one described by JANCZEWSKI. GOEBEL'S illustration would lead us to believe that the canal row has been formed by the activity alone of the one cell marked +. This is most certainly not the method of canal row formation described by JANCZEWSKI. Hence GOEBEL must be regarded as giving an entirely different account for the development of the canal row.

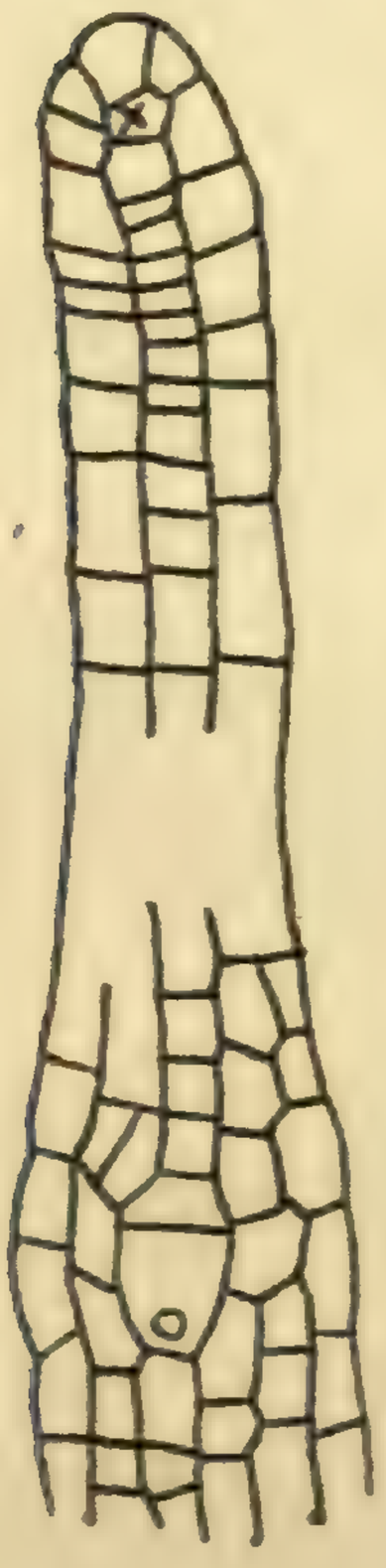

FIG. 1.—Archegonium of *Mnium undulatum*, reproduced from GOEBEL'S *Organography, fig. 8, iv+*.

HOLFERTY (7) in 1904 made a critical study of the archegonium of *Mnium cuspidatum*. Here for the first time we have evidence somewhat scanty, but thoroughly convincing so far as it goes, because based on the sure foundation of division figures. In the development of the canal row HOLFERTY found once, and figures, the cover cell adding to the canal row. In 3 other archegonia he shows the topmost canal cell in the process of division, while in one case the basal neck canal cell is dividing.

Regarding the development of the archegonium proper his summary is as follows (p. 122):

6. In the young archegonium the 2-sided apical cell gives place to a 3-sided one which is truncate.

7. This terminal cell divides transversely soon after its formation giving rise to the first cell of the axial row.

8. The terminal cell adds to the growth of the neck by segments cut from its 3 lateral faces, and to the growth of the axial row by segments cut from its truncate face.

9. Growth in length of the archegonium neck is intercalary as well as apical in both neck and canal rows.

SERVETTAZ (13) in a quite recent physiological paper on the Musci includes an investigation of the development of *Phascum cuspidatum*. The developmental story is given briefly as follows (p. 171):

La cellule initiale se cloisonne transversalment et donne une cellule de peid, "a," et une cellule supérieure "b"; la cellule "b" se cloisonne ensuite obliquement un certain nombre de fois (2–5) comme s'il s'agissait de constituer un bourgeon végétatif ordinaire, puis l'une des cellules placées au-dessous de la cellule terminale se divise tangentiellement et détermine la formation d'une cellule central "c" qui, par des cloisonnements basipètes, donne une file de 8 cellules qui seront: 1–4, les cellules du canal; 5, la cellule du ventre; 6, l'oosphere. . . .

Quant à la cellule terminale, "s," elle peut continuer à se diviser et elle forme la calotte recouvrant l'extrémité du col.

En definitive, le mode de formation que nous venons de décrire se rapproche de celui que Goebel a décrit pour Mnium undulatum.

The evidence offered in support of this developmental story is certainly too meager and not sufficiently critical to be convincing. Moreover, the origin of the central cell, or first cell of the axial row, by a tangential division of one of the segments below the terminal cell is a revival of the HOFMEISTER conception which numerous subsequent investigations have failed to confirm, both in the Hepaticae and in the Musci. It would be nothing less than remarkable, therefore, to find the origin of the archegonium proper in *Phascum* fundamentally different from that of the other Musci.

In 1915 the author (1) published his studies on the archegonium of *Sphagnum subsecundum*. From sections both transverse and longitudinal it was shown that the archegonium proper is initiated in the terminal cell by the appearance of 3 oblique walls, which cut off 3 peripheral segments and produce the axial cell within. This latter cell on division gives rise to the cover cell and the central cell. Clear evidence is presented that the cover cell is relatively inactive, forming no basal segments, while division figures

make it certain that the growth of both canal row and peripheral cells of the neck is intercalary and not apical.

SUMMARY

In regard to the formation of the archegonium proper in the Musci 3 theories have been advanced: (1) the HOFMEISTER conception of the tangential division of one of the 4 original pedicel rows, a theory soon made untenable by the work of later investigators; (2) a recent revival of the HOFMEISTER scheme modified by the tangential division of one segment only, as proposed by SERVETTAZ; (3) the commonly accepted account, confirmed again and again for all the great groups of the Bryophyta, namely, the appearance in the terminal cell of 3 oblique walls forming 3 peripheral segments and an axial cell within.

It cannot be maintained, therefore, that the origin of the archegonium proper is in doubt. The evidence is too overwhelming to admit of any uncertainty on this point. However, the development of the axial row is another matter. Here is a subject involving widely conflicting accounts, some being diametrically opposed. Summarized, these accounts are: (1) the abandoned conception of HOFMEISTER, having only a historic interest; (2) KÜHN's claim for *Andreaea* that all the cells of the axial row are cut from the base of the apical cell; (3) CAMPBELL states for *Funaria* that the axial row is composed of a primary canal cell and segments cut from the base of the apical cell, none of which divide after they are formed, so far as could be determined; (4) GOEBEL holds that in *Mnium undulatum* the topmost neck canal cell (the one just below the cover cell) acts as an apical cell in the production of the canal row; (5) JANCZEWSKI finds that the cells of the axial row are of diverse origins, the upper arising through transverse divisions of the 2–6 initials cut from the base of the apical cell, while the lower are formed by the transverse divisions of the primary canal initial; (6) HOLFERTY has shown that the growth in the canal row of *Mnium cuspidatum* is both apical and intercalary; (7) GAYET concludes that the canal cells among the Musci have all the same origin, that there are no segments cut from the base of the apical cell, but that the whole axial row arises from an

initial produced by the mother cell of the egg; (8) SERVETTAZ states that in *Phascum* the canal row is formed by the basipetal divisions of the central cell; (9) the author has shown by division figures that in *Sphagnum subsecundum* the growth of the canal row is entirely intercalary.

It is evident that the Bryales are in need of a reinvestigation, not a superficial examination of many forms, but a careful intensive study of representative forms showing as far as possible by actual division figures the course of development. It is with such an idea in mind that the present work has been undertaken.

Development of archegonium

The apparently dioecious *Catharinea angustata* here studied produces a fairly large number of archegonia on each gametophore. The count shows variability with an average of about twenty. As previously stated, young archegonia begin their appearance early in April, and by the middle or end of May the majority have reached maturity. The first archegonium arises from the apical cell region, but whether from the apical cell itself or from one of its immediate segments cannot be stated positively at present. The study of the behavior of the apical cell in the production of archegonia and the continued growth of the gametophore, if fertilization does not occur, must be reserved for a later paper. In its early stages the archegonium develops by the usual method of an apical cell with two cutting faces (figs. 1, 3–5, 7–9). In the large amount of material examined only two exceptions to this statement have been found (figs. 2, 6). In both cases the young archegonia were developing in very crowded quarters, being closely surrounded by the stalks of archegonia nearing maturity.

After a variable number of segments, usually 4 or 5, have been produced by the apical cell, and secondary divisions have appeared in each segment except the terminal one, the plane of division changes. In the terminal cell, as so often described both for Hepaticae and Musci, 3 oblique walls cut off peripheral segments and originate the primary axial cell within. In fig. 10 the first oblique wall has been formed; in fig. 11 two of the oblique walls are shown. These oblique walls usually do not intersect, as CAMPBELL reports

for *Funaria*, but extend to the basal walls. The primary axial cell, therefore, has something of the shape of an inverted, truncated pyramid. There now follows the division of the primary axial cell into an outer axial cell, the cover cell, and an inner axial cell, the central cell (figs. 12, 13). Quite soon the central cell divides, the resulting lower cell being the ventral cell, while the upper is the primary neck canal cell (figs. 14, 15). The actual division of the central cell was found twice. The axial row of the young archegonium now consists of the ventral cell; its sister cell, the primary neck canal cell; and a large cover cell (figs. 15–17).

It is interesting to note that in fig. 15 the original division wall between cover cell and central cell appears tilted, due partly to the inequality in the growth of the peripheral segments, and partly to the change in the direction of the axis through the formation of new peripheral segments by the apical cell. While this tilting is not always found, it is of frequent occurrence, as shown to a greater or less extent in figs. 16, 18, 20, and furnishes valuable evidence in separating that portion of the axial row derived from the central cell from the part contributed by the cover.

The cover cell now cuts off peripheral segments (figs. 15–17). No absolute proof can be given as to their exact number, but it seems more than probable from such a series as figs. 15–18 that there are 3 peripheral segments. Then there is added to the canal row an initial cut from the base of the cover cell. The evidence for this statement rests on fig. 18, on several others quite like it, and is corroborated by the figures in the series about it (figs. 16–20). Several similar series could be constructed from the material studied. A long and careful search failed to reveal the actual division figure, but in fig. 18 the size and position of the nuclei and the delicate wall between leave no doubt that the uppermost canal cell has been cut from the base of the cover cell and that the process has just been completed. As illustrated by fig. 19 the axial row now consists of the ventral cell; its sister cell, the primary neck canal cell; an initial cut from the base of the cover cell; and a large cover cell or apical cell.

Up to this point the process of development is clear and definite; but from this point on there is a variability shocking to no

one save an old-fashioned, rigid morphologist. After the first initial has been added to the canal row, the apical cell again begins to cut off peripheral segments (figs. 20, 23), but in the meanwhile the periphery is also growing by intercalary divisions (figs. 19, 20, 22). While these peripheral processes are going on, the cells of the neck canal row are not inactive. The primary neck canal cell may divide first (figs. 20, 21), or the initial cut from the base of the cover cell may make the first division (fig. 22). That there are intercalary divisions in almost any order at this stage of the process may clearly be seen from the series represented by figs. 25–28. The archegonium has now reached the stage when it contains 4 or 5 neck canal cells. At this time the evidence is positive that the cover cell adds a second initial to the row of neck canal cells (figs. 29, 31). Fig. 29 illustrates excellently the intercalary as well as apical growth of the archegonium.

While fig. 31 is of interest in showing the activity of the cover cell in adding an initial to the canal row, it has an additional interest in giving evidence as to the origin of oblique walls in the axial row. The axis of the spindle is tilted and an oblique wall is being formed. In fig. 32 the process has been completed and the result is very evident. There are then two origins for the oblique walls in the canal row. The first we have mentioned in connection with fig. 15. No reliable evidence could be found that these walls might arise in any other way, such, for example, as the intercalary division of a canal cell. As a result of intercalary as well as apical activity the canal row now contains 5–7 canal cells. In the events that follow there is no definite sequence that can be determined. The only positive statement that can be made is that the number of canal cells is increased by intercalary divisions and in practically any order (figs. 33–45).

Just how active the cover cell is at this time cannot be stated, but the numerous figures in the canal row and the periphery of the neck make it evident that intercalary divisions are responsible in a large measure for the growth of the archegonium. In figs. 42, 44, it seems very probable that in each case the topmost canal cell has been cut from the base of the cover cell. No division figure could be obtained, so that a positive assertion cannot be made.

Fig. 48 shows the formation of what is probably in the majority of cases a last initial cut from the base of the cover cell. Abundant evidence has been found that at some time between the 12–16 neck canal cell stage the cover cell changes its manner of division and segments by a wall perpendicular to its base into two more or less equal parts (figs. 50, 51, 54, 56). The division figure was found once and is shown in fig. 56. No evidence could be obtained that the division may occur before the 12 neck canal cell stage; while after the 16 neck canal cell stage practically all covers showed division. Out of the large number of cases studied only two exceptions were found, one a case of 18 neck canal cells, and the other a case of 20 with the cover in each yet undivided. Such a process, then, while occurring within general limits is by no means fixed. Whenever such a division does occur, it signalizes the end of all true apical activity. The segmented cover stands out well defined from the peripheral segments of the neck and its history can be followed for some time with a reasonable degree of accuracy. Thus in figs. 61 and 62 the cover cell has formed 6 segments (3 shown in median longitudinal section) and is literally the cap of the archegonium. In fig. 72*A* we have the cross-section of the cover of an archegonium containing 35 neck canal cells. It shows clearly the primary division wall 1–1; the quadrant walls 2–2; and the subsequent divisions in each quadrant. When the archegonium is fully matured the segments of the cover merge insensibly with those of the neck, hence an exact statement cannot be made as to the final number produced.

The division of the ventral cell into ventral canal cell and egg was found five times, 3 being shown (figs. 47, 50, 53). Here again one finds the same sort of variability noted for the cover cell, but with a slightly greater range. The division may occur as early as the 11 neck canal cell stage (fig. 47), while several cases were found in which there were 17–20 neck canal cells with the venter yet undivided (figs. 58, 60). The ventral canal nucleus formed by this division is quite variable in size. Sometimes it is about the same size as the egg (figs. 56, 61, 68); or it may be noticeably smaller (figs. 54, 59, 62).

As already stated, the cutting off of initials from the base of the cover cell is in the majority of cases brought to a conclusion some-

where between the 12 and 16 neck canal cell stages; but since the undivided cover cell may be found as late as the 20 neck canal cell stage, it is evident that a variable number of initials may be cut from its base. We have given proof that at least 3 initials are produced, but we can make no positive statement as to the maximum number. By making due allowance for the rapid intercalary growth, we should estimate that in the majority of cases the number does not exceed 5 or 6.

Whatever may be the number of initials, the fact remains that both the canal row and the peripheral cells of the neck continue to grow by intercalary divisions. Figs. 45–61 show some of the many divisions found and furnish ample proof for the statement. This continued intercalary growth finally produces an astonishingly large number of neck canal cells. In the material studied the average count is well over 50; frequent examples in the sixties were found; two in the seventies (one with 74 and the other with 76 neck canal cells); and finally one example in which there were 86 neck canal cells with several of the basal neck canal cells just beginning to disintegrate. Not only is the number of neck canal cells large, but the canal row is generally multiple in its upper part (fig. 65). Less often this multiplicity is found through the middle portion of the neck (fig. 66) and in the basal part of the canal row (fig. 68). We have interesting evidence from fig. 64 that this multiple condition may arise by the simultaneous division of the cells concerned.

A study of cross-sections through mature archegonia furnished some interesting facts. A representative series through the terminal portion of the neck is shown in fig. 69*A–F*. The canal row is not merely double in this portion but generally consists of 3 cells and in some cases 4. The peculiar enlargement of the canal at its upper end is well shown by figs. 65, 69. The breaking down of the canal row in all of the cases observed was acropetal, but did not involve the ventral canal cell. This latter cell persists for some time, but its history up to fertilization has not been followed as yet. The venter of the mature archegonium is not uniform in thickness, but shows variations from 2 to 4 cells (fig. 63).

ABNORMALITIES.—In the large amount of material studied there was a striking lack of the so-called abnormalities. Only

two cases were found, one being illustrated in fig. 70. The archegonium here contains 17 neck canal cells, 3 of which are shown, and has 3 cells in the venter. It seems probable that the 2 lower ones were formed by the division of the egg, while the upper is the ventral canal cell which has remained undivided. Fig. 71 is the reconstruction of a very remarkable double archegonium. It may have originated by the fusion of 2 very young archegonia, or by the longitudinal instead of transverse division of the primary axial cell.

Discussion

Catharinea undulata has been studied by JANCZEWSKI only. The present work on the closely related *C. angustata* confirms in general his statements, especially in reference to the origin and development of the canal row. There can be no doubt that the cells of the neck canal row in *C. angustata* are of diverse origins. The lower arise through intercalary divisions of the primary neck canal cell, while the upper are produced by the intercalary divisions of at least 3 initials cut from the base of the cover cell.

Aside from the activity of the cover cell, there is no evidence that any *one* neck canal cell may act as an apical cell in the development of the canal row. On the contrary, the evidence is clear that *any* cell of the neck canal row may divide and in any order. This process is also in general agreement with the findings of HOLFERTY for *Mnium cuspidatum*, where both apical growth and intercalary divisions are reported. If CAMPBELL is correct, *Funaria* shows a striking difference, in that the primary canal cell and the initials cut from the base of the apical cell do not divide after they have been formed; while GOEBEL'S account for *Mnium undulatum* shows still further difference, in that one of the neck canal cells at the apex of the canal row becomes an apical cell and by its activity produces the further growth of the canal row. If these differences are confirmed, we shall have a remarkably interesting series in archegonial development.

The facts in the present paper furnish an emphatic denial of the sweeping generalization of GAYET that among the Musci the cover cell does not give rise to neck canal cells. While the author has shown in a previous paper that in *Sphagnum subsecundum* no

initials are added to the canal row by the cover cell, this investigation makes it certain that in *Catharinea angustata* at least 3 initials are produced. Just what type of development the representatives of other groups of the Bryales will show remains to be seen.

Conclusions

The archegonium of *Catharinea angustata* grows for a time by apical as well as intercalary divisions in both canal row and peripheral cells of the neck. In its later stage the entire growth is intercalary.

The cells of the canal row have a double origin. The lower are formed by the intercalary divisions of the primary neck canal cell, the upper through the intercalary divisions of the 3 or more initials cut from the base of the cover cell.

How general this condition is among the Bryales must await further work.

Summary

1. The archegonia of *Catharinea angustata* begin to develop in April.

2. The first formed archegonium arises from the apical cell region, but whether fron the apical cell itself or from one of its immediate segments must be determined later.

3. In the earlier stages of development the young archegonium is formed by the activity of an apical cell with two cutting faces producing a filament of a few cells.

4. The archegonium proper is initiated by the appearance in the terminal cell of 3 oblique walls cutting off 3 peripheral segments and originating the primary axial cell within, which on division gives rise to the cover cell and the central cell.

5. The central cell on division forms the primary neck canal cell and the ventral cell.

6. The cover cell is active for a time, cutting off peripheral segments for the outer cells of the neck and basal initials for the canal row.

7. The number of basal initials varies, but is at least 3 in *Catharinea undulata*.

8. The cells of the canal row and the peripheral cells of the neck grow by intercalary divisions, and in any order.

9. The major growth of the archegonium is intercalary.

10. The cells of the neck canal row have a double origin. The lower are formed by the intercalary divisions of the primary neck canal cell; the upper through the intercalary divisions of the 3 or more initials cut from the base of the cover cell.

11. The ventral cell divides relatively early into ventral canal cell and egg.

12. The ventral canal cell is variable in size.

13. The mature archegonium has usually more than 50 neck canal cells, and may contain as many as 86.

14. The canal row is generally multiple in its upper part and occasionally throughout.

15. The disintegration of the canal row is acropetal, but does not involve the ventral canal cell.

16. If the number of neck canal cells is an indication of primitiveness, the most advanced group of the mosses has the most primitive archegonium yet described among the Bryophyta.

UNIVERSITY OF WISCONSIN

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EXPLANATION OF PLATES I–VIII

All figures were drawn with the aid of Abbé camera lucida at table level, and, being reduced one-half in reproduction, now show the following magnifications: figs. 1–27, ×870; figs. 28–35, 64–68, ×700; figs, 36–44, 63, 69, 70, 72–74, ×550; figs. 45–62, ×410; fig. 71, ×225. Abbreviations are as follows: *a*, base of older archegonium; *l*, leaf; *p*, paraphysis.

PLATE I

FIG. 1.—First archegonium arising from apical cell region.

FIG. 2.—Young archegonium with abnormal cross walls arising at base of older archegonia.

FIG. 3.—Typical development by apical cell with 2 cutting faces.

FIG. 4.—The same, slightly older.

FIG. 5.—The same, still older.

FIG. 6.—Development by walls which do not quite intersect; bases of older archegonia seen on each side of young archegonium.

FIG. 7.—Typical development, older stage.

FIG. 8.—The same.

FIG. 9.—The same; relation to apical cell well shown.

FIG. 10.—First archegonium arising from apical cell region which has now segmented irregularly; in terminal cell the first of the 3 oblique walls originating the archegonium proper has been formed.

FIG. 11.—In terminal cell the 3 oblique walls have cut off peripheral segments and formed primary axial cell within.

FIG. 12.—Primary axial cell has divided into cover cell and central cell.

FIG. 13.—The same, slightly older.

FIG. 14.—Central cell dividing to form primary neck canal cell and ventral cell.

FIG. 15.—Division of central cell has just been completed; cover cell has formed a peripheral segment on the right.

PLATE II

FIG. 16.—Primary neck canal and primary ventral cell.

FIG. 17.—The same; cover cell has formed 3 peripheral segments, 2 being shown.

FIG. 18.—Two neck canal cells and ventral cell; topmost neck canal cell is the first initial cut from base of cover cell and has just been formed.

FIG. 19.—Two neck canal cells and ventral cell, later stage.

FIG. 20.—Two neck canal cells and ventral cell; cover cell forming a peripheral segment, while primary neck canal cell is in division.

FIG. 21.—Two neck canal cells and ventral cell; primary neck canal cell in division.

FIG. 22.—Two neck canal cells and ventral cell; first initial cut from base of cover in division.

FIG. 23.—Two neck canal cells and ventral cell; cover cell forming a peripheral segment.

FIG. 24.—Three neck canal cells and ventral cell.

FIG. 25.—Three neck canal cells and ventral cell; middle neck canal cell in division.

FIG. 26.—Three neck canal cells and ventral cell; topmost neck canal cell in division.

FIG. 27.—Four neck canal cells and ventral cell.

PLATE III

FIG. 28.—Four neck canal cells and ventral cell; second neck canal cell from ventral cell in division.

FIG. 29.—Four neck canal cells and ventral cell; simultaneous division of basal and topmost neck canal cell, while cover cell adds a second initial to canal row.

FIG. 30.—Four neck canal cells and ventral cell; cover cell forming peripheral segment.

FIG. 31.—Four neck canal cells and ventral cell; cover cell adding second initial to canal row.

FIG. 32.—Five neck canal cells and ventral cell; topmost neck canal cell cut from base of cover cell.

FIG. 33.—Five neck canal cells and ventral cell; second neck canal cell from ventral cell in division.

FIG. 34.—Five neck canal cells and ventral cell; topmost neck canal cell in division.

FIG. 35.—Five neck canal cells and ventral cell; basal neck canal cell in division.

PLATE IV

FIG. 36.—Six neck canal cells and ventral cell.

FIG. 37.—Six neck canal cells and ventral cell; topmost neck canal cell in division.

FIG. 38.—Seven neck canal cells and ventral cell; second neck canal cell from ventral cell in division.

FIG. 39.—Seven neck canal cells and ventral cell; fifth neck canal cell from ventral cell in division.

FIG. 40.—Eight neck canal cells and ventral cell; fourth and fifth neck canal cells from ventral cell in simultaneous division; topmost neck canal cell probably cut from cover cell.

FIG. 41.—Eight neck canal cells and ventral cell; basal canal cell in division; marked intercalary growth in the peripheral cells of the neck.

FIG. 42.—Nine neck canal cells and ventral cell; middle neck canal cell in division; topmost neck canal cell probably cut from base of cover cell.

FIG. 43.—Nine neck canal cells and ventral cell; fourth neck canal cell in division.

FIG. 44.—Nine neck canal cells and ventral cell; fourth and sixth neck canal cells from ventral cell in simultaneous division.

PLATE V

FIG. 45.—Ten neck canal cells and ventral cell; ninth neck canal cell in division.

FIG. 46.—Eleven neck canal cells and ventral cell; ninth and tenth neck canal cells in simultaneous division.

FIG. 47.—Eleven neck canal cells with ventral cell in division to form ventral canal cell and egg.

FIG. 48.—Eleven neck canal cells and ventral cell; cover cell adding an initial to canal row.

FIG. 49.—Eleven neck canal cells and ventral cell; second neck canal cell from ventral cell in division.

FIG. 50.—Twelve neck canal cells with ventral cell in division; cover cell has divided into 2 almost equal segments; apical activity ended.

FIG. 51.—Twelve neck canal cells, ventral canal cell, and egg; cover cell divided; apical activity ended.

FIG. 52.—Thirteen neck canal cells and ventral cell; ninth neck canal cell in division.

FIG. 53.—Thirteen neck canal cells with ventral cell in division; seventh, ninth, and tenth neck canal cells in division.

FIG. 54.—Thirteen neck canal cells, ventral canal cell and egg; eighth neck canal cell in division; cover divided.

PLATE VI

FIG. 55.—Thirteen neck canal cells and ventral cell; intercalary growth in peripheral cells of neck.

FIG. 56.—Fourteen neck canal cells, ventral canal cell and egg; ninth and tenth canal cells from ventral cell in division; cover cell dividing into 2 almost equal segments by wall perpendicular to base; apical activity now brought to an end.

FIG. 57.—Fourteen neck canal cells and ventral cell; ninth neck canal cell from ventral cell in division.

FIG. 58.—Eighteen neck canal cells and ventral cell; seventh and eighth neck canal cells from ventral cell in division; cover shows 3 segments in median longitudinal section.

FIG. 59.—Eighteen neck canal cells, ventral canal cell, and egg; eleventh and twelfth neck canal cells in division.

FIG. 60.—Twenty neck canal cells and ventral cell; fifth and sixth neck canal cells in division; peripheral cells showing intercalary divisions.

FIG. 61.—Thirty neck canal cells, ventral canal cell, and egg; 2 uppermost neck canal cells in division; cover shows 3 segments in median longitudinal section.

FIG. 62.—Forty-three neck canal cells, ventral canal cell, and egg; cover shows 3 segments in median longitudinal section.

FIG. 63.—Cross-section of venter of mature archegonium at level of egg, showing variable number of cells in thickness.

PLATE VII

FIG. 64.—Terminal portion of an archegonium approaching maturity with the 10 neck canal cells in simultaneous division.

FIG. 65.—Terminal portion of an archegonium approaching maturity showing marked enlargement of canal and multiple condition of canal row.

FIG. 66.—Middle portion of neck of an archegonium showing multiplication of neck canal cells.

FIG. 67.—Lower portion of an archegonium nearly mature showing 3 neck canal cells in simultaneous division.

FIG. 68.—Lower portion of an archegonium practically mature showing multiplication of canal cells; ventral canal cell and egg almost equal in size.

FIG. 69.—Series of transverse sections through terminal portion of a mature archegonium showing multiple condition of neck canal row.

PLATE VIII

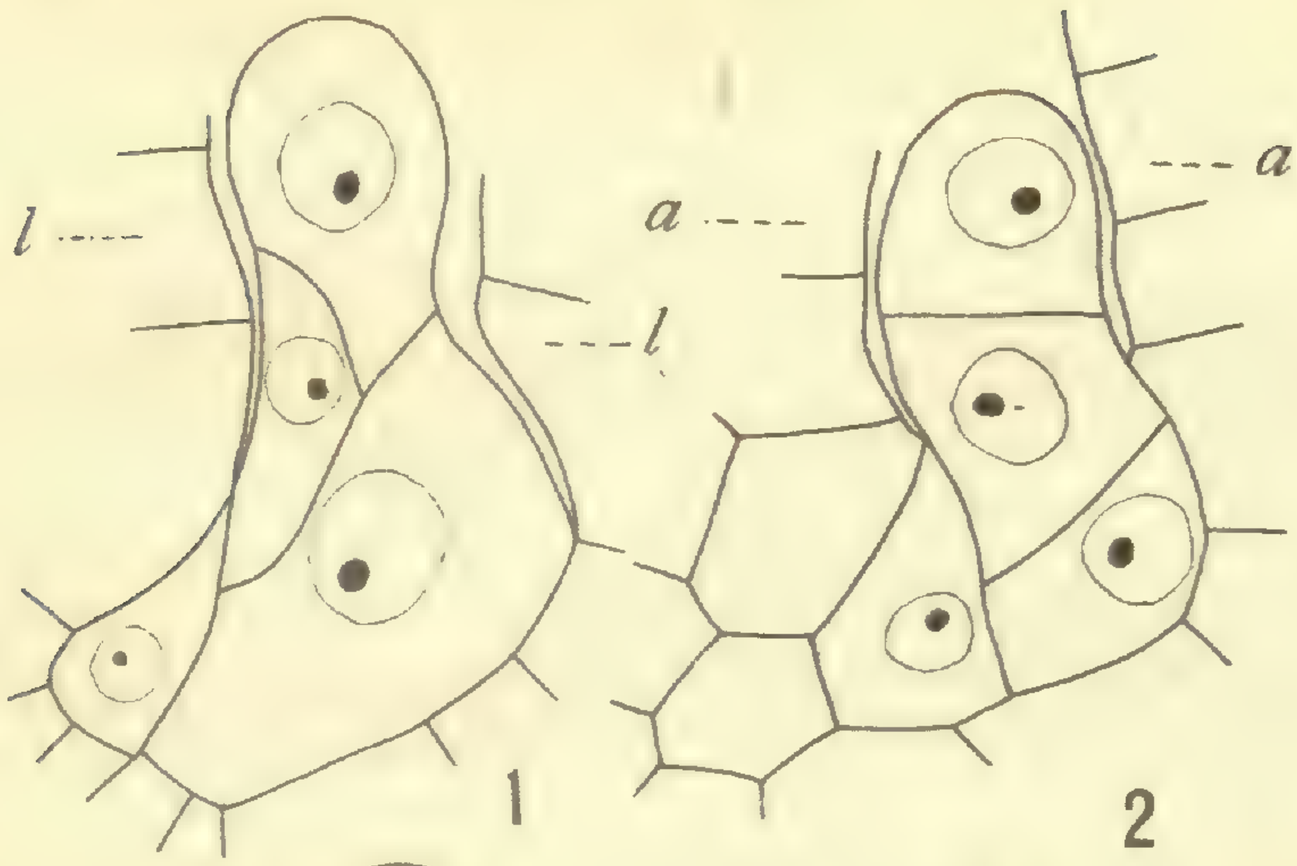
FIG. 70.—Venter with 3 cells, 2 lowest are probably eggs; uppermost is probably ventral canal cell.

FIG. 71.—Double archegonium.

FIG. 72.—Serial sections through upper part of an archegonium containing 35 neck canal cells, ventral canal cell and egg; section *A* shows in cover cell: 1–1, primary division wall; 2–2, quadrant division; and further division in each quadrant; series shows variations in number of peripheral cells of neck.

FIG. 73.—Serial sections through middle portions of neck of same archegonium showing remarkable regularity in number of peripheral cells of neck.

FIG. 74.—Serial sections through lower portion of same archegonium showing thickness just above venter (*A–D*); venter at level of ventral canal cell (*E*); venter at level of egg (*F*).



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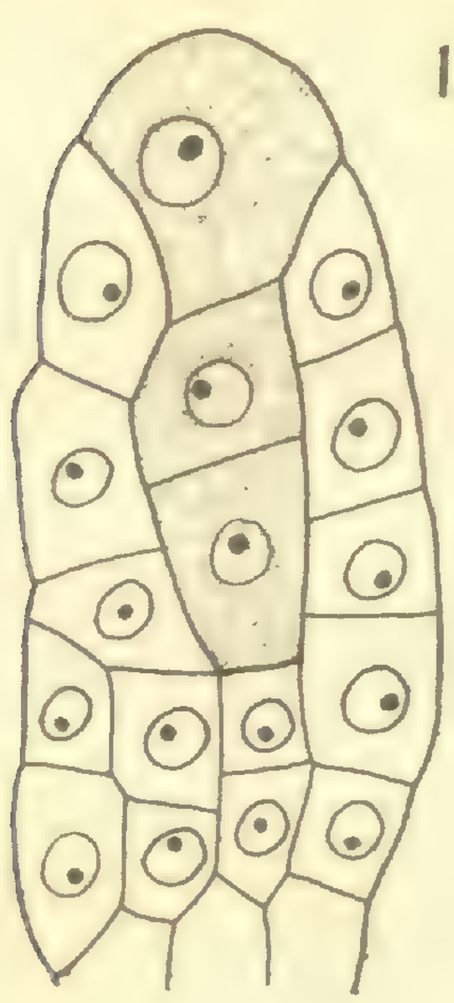

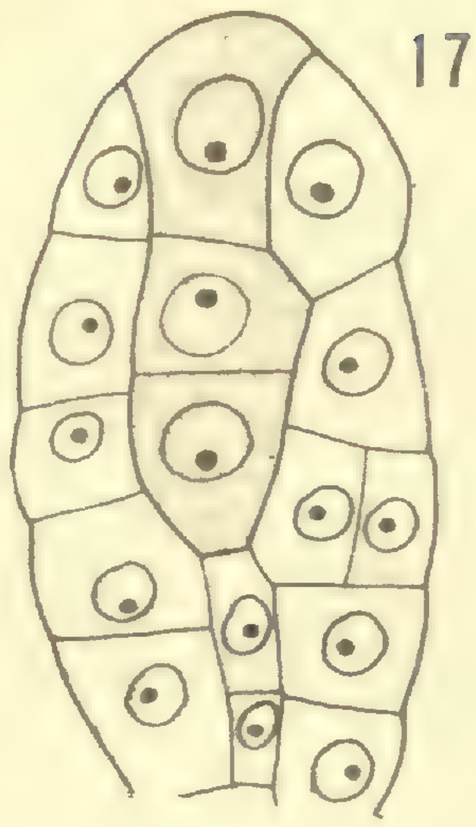

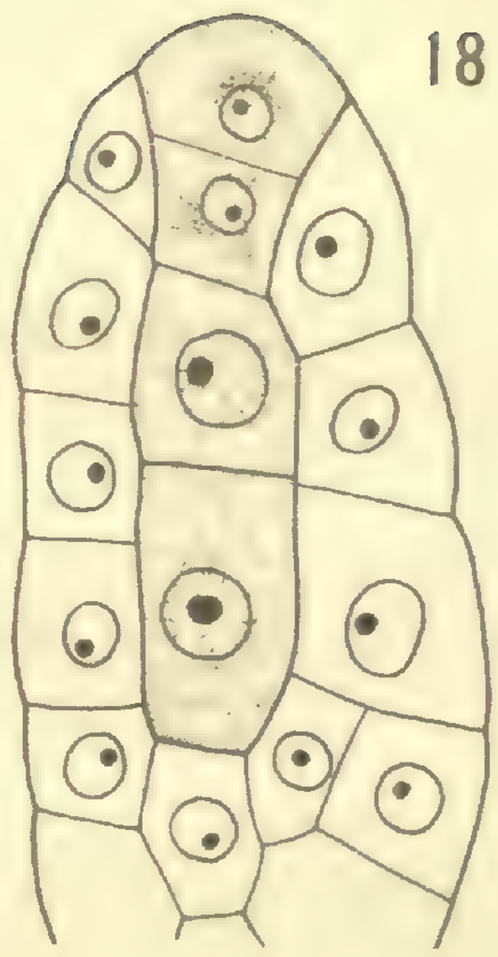

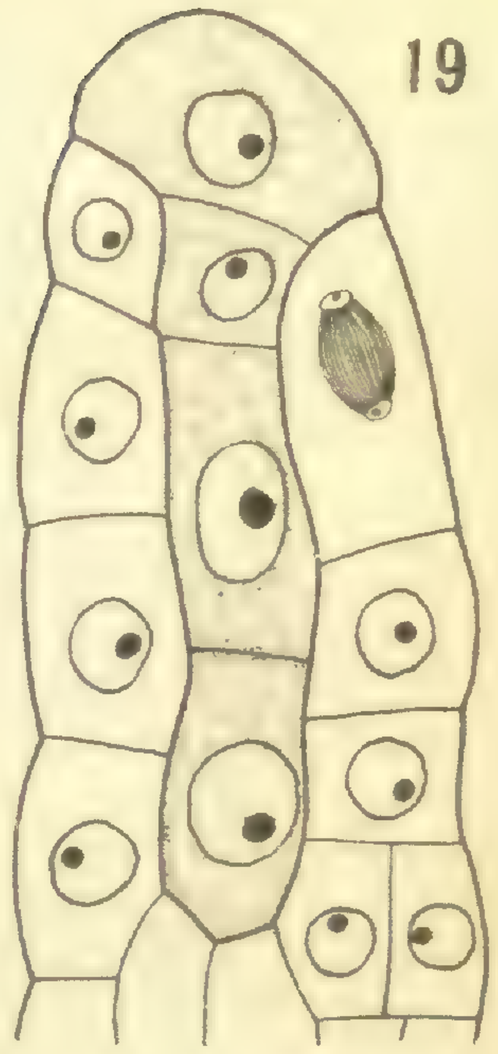

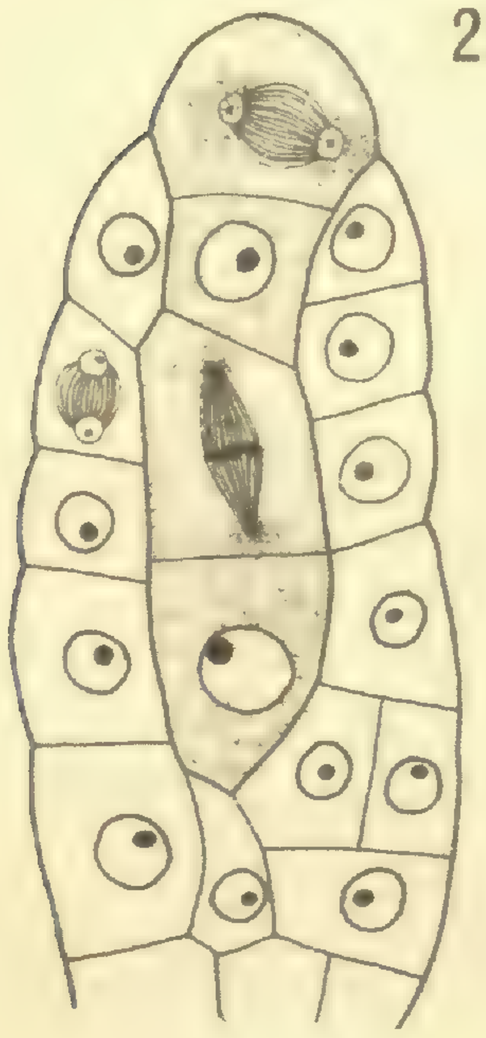

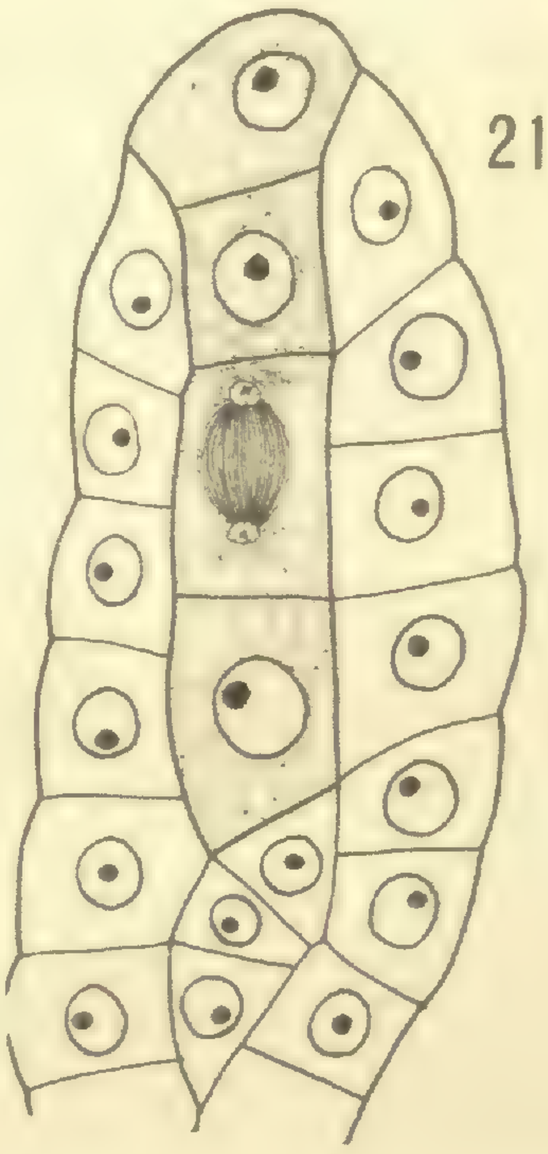

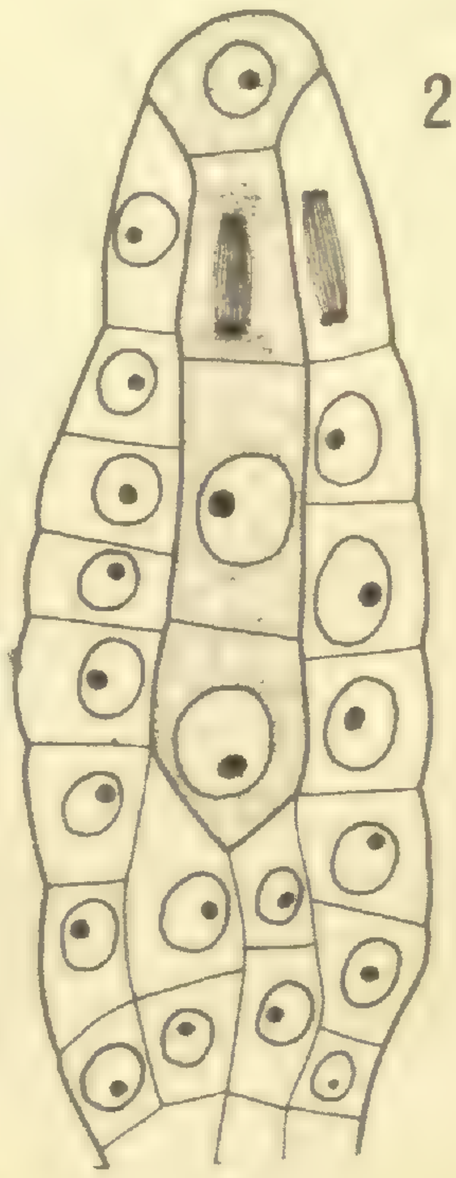

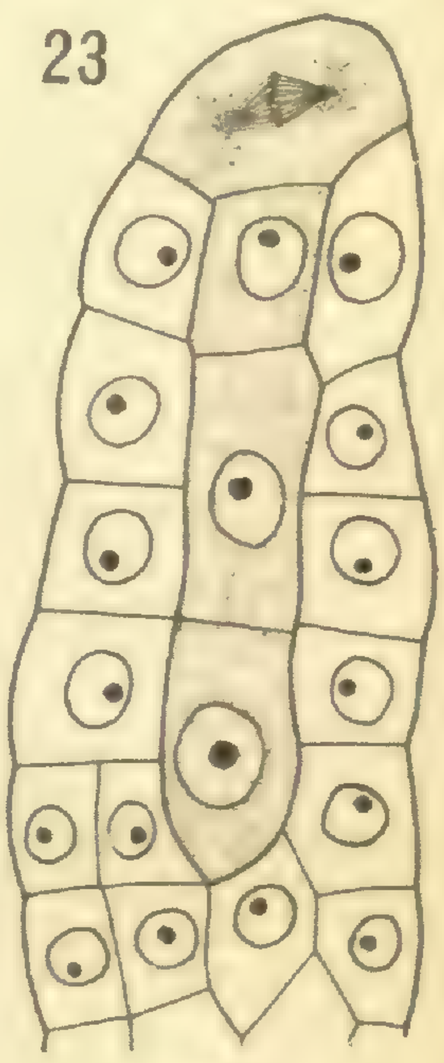

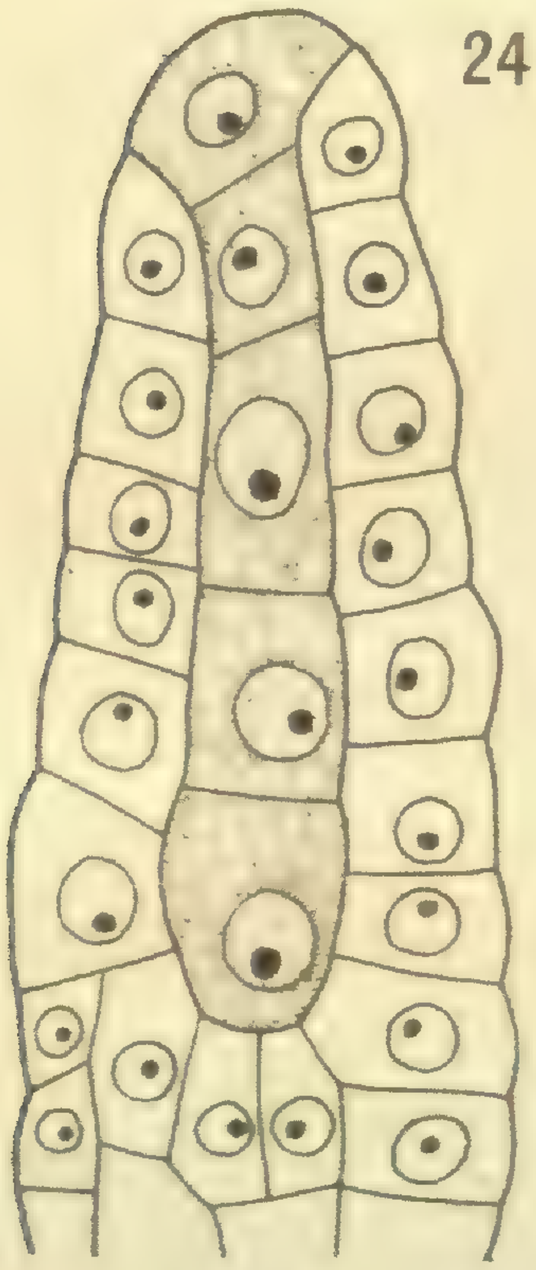

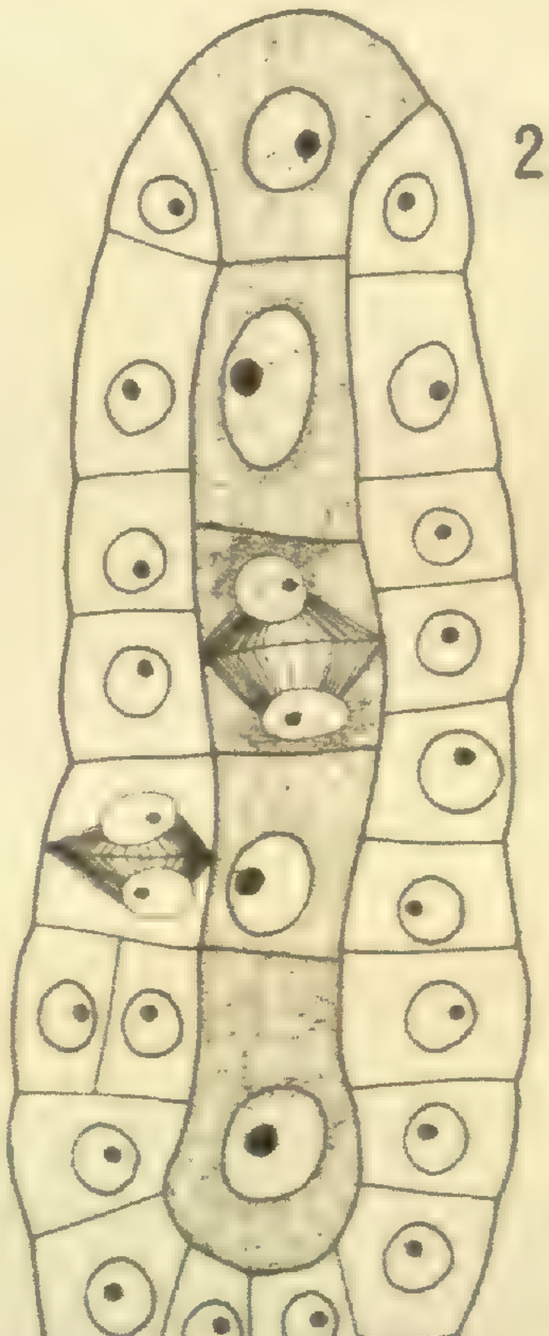

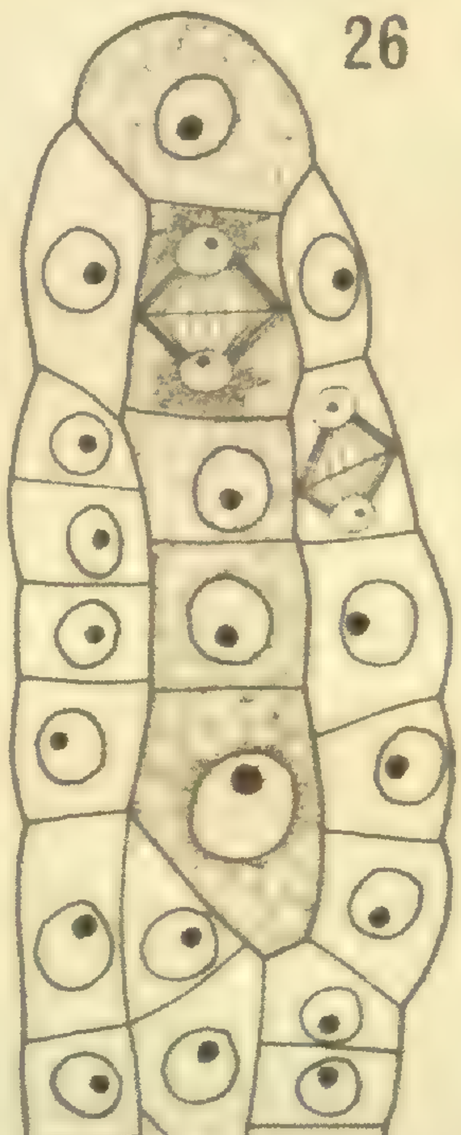

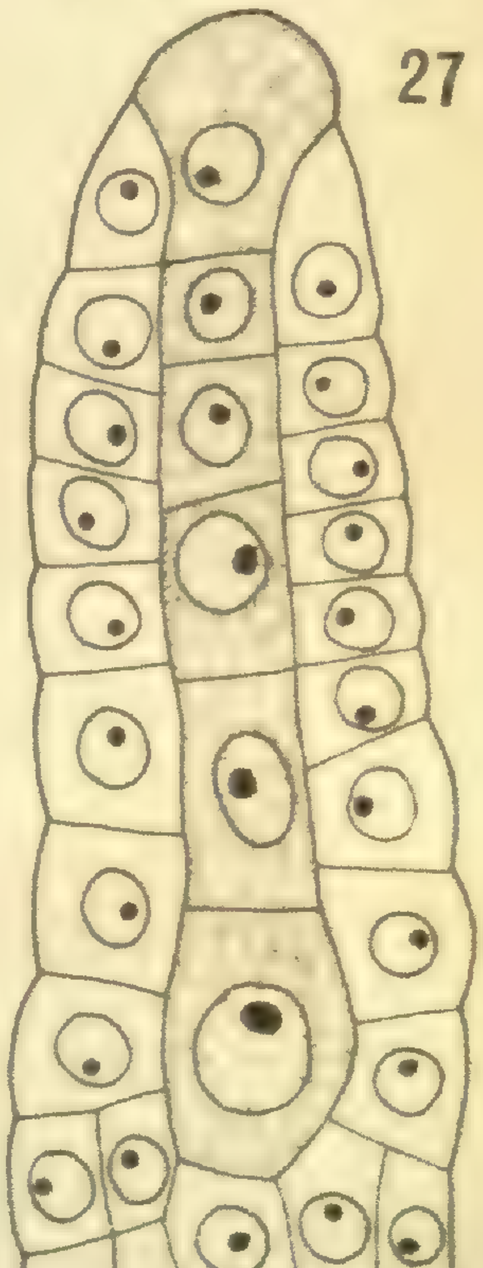

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BRYAN on CATHARINEA

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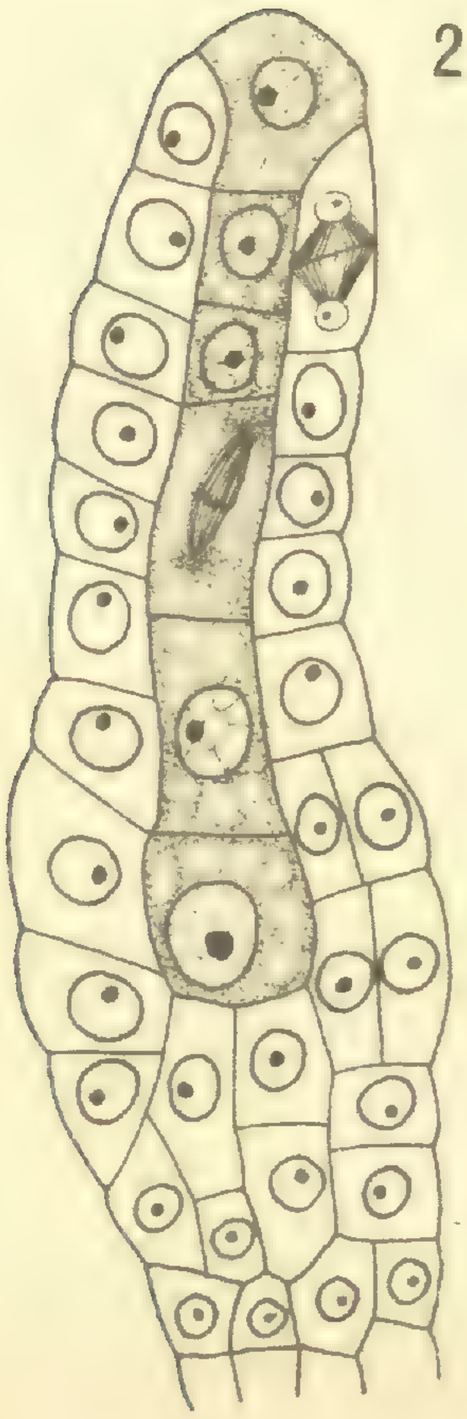

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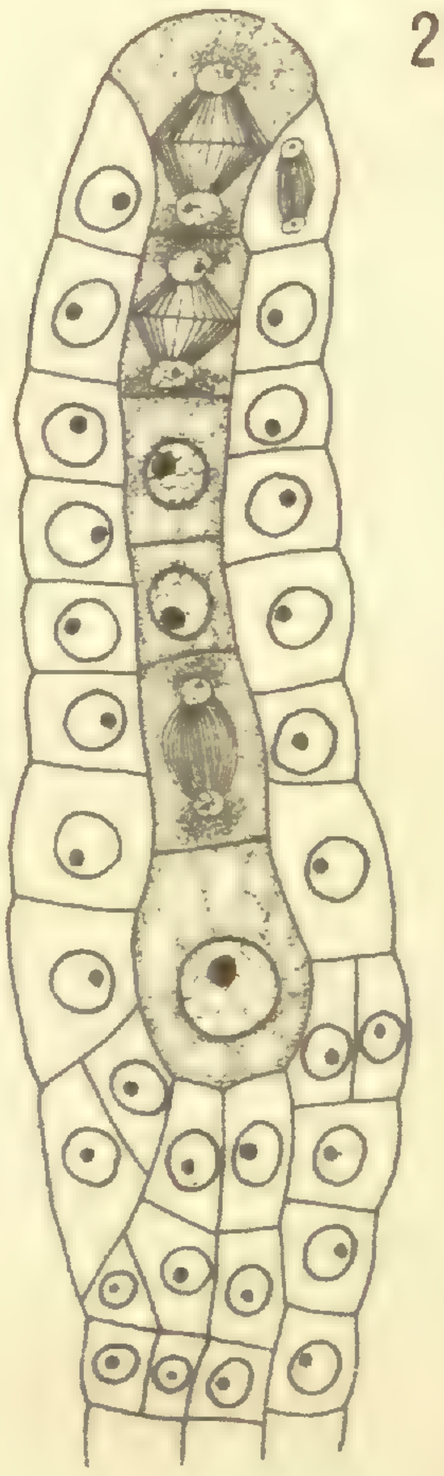

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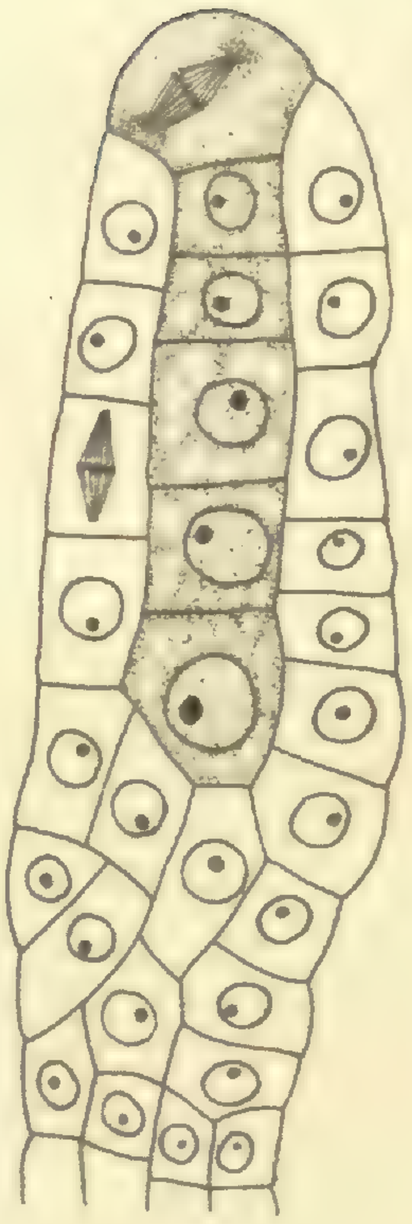

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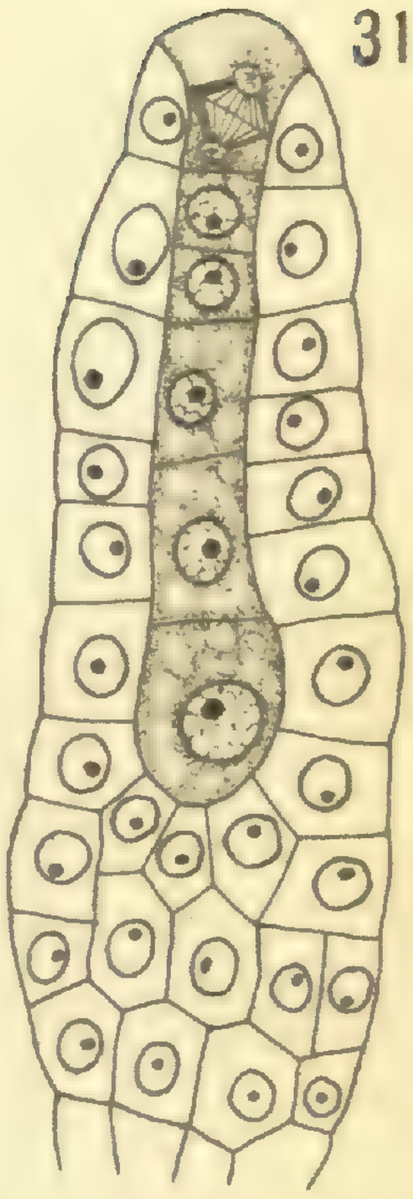

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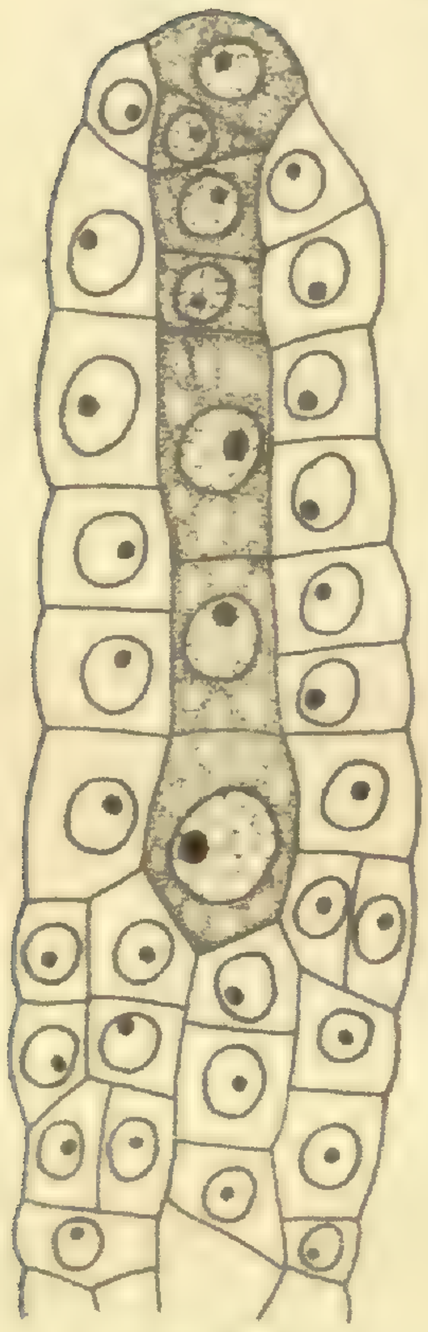

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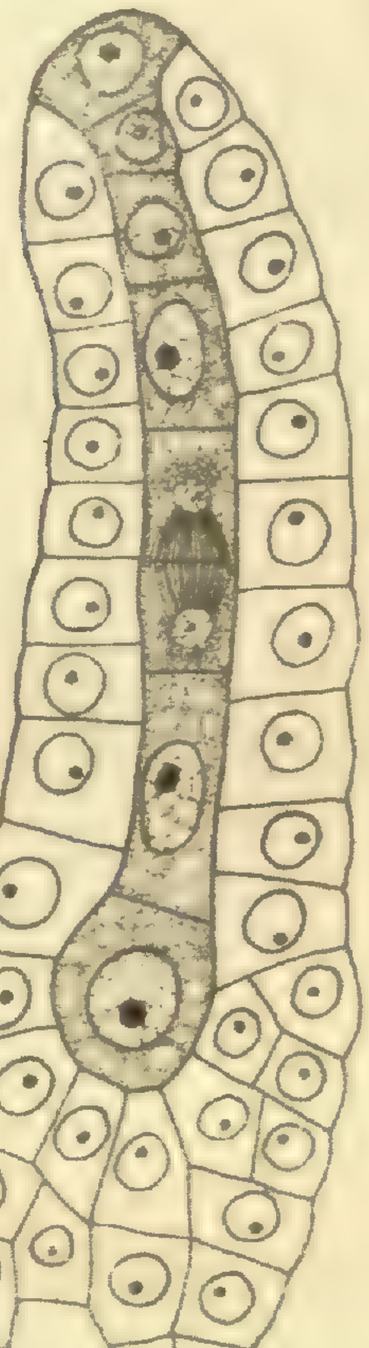

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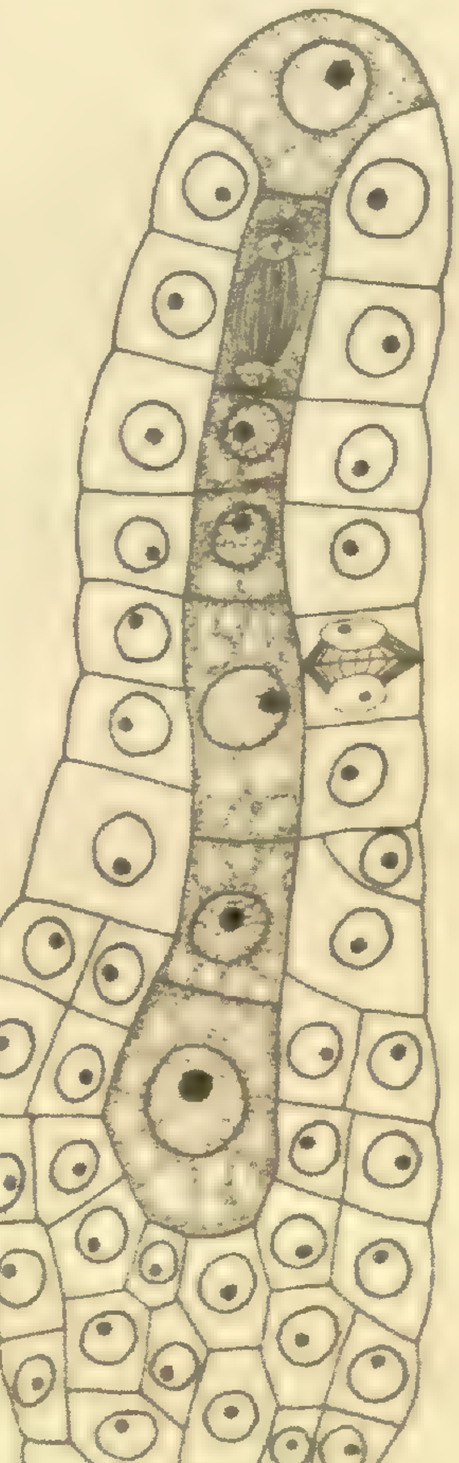

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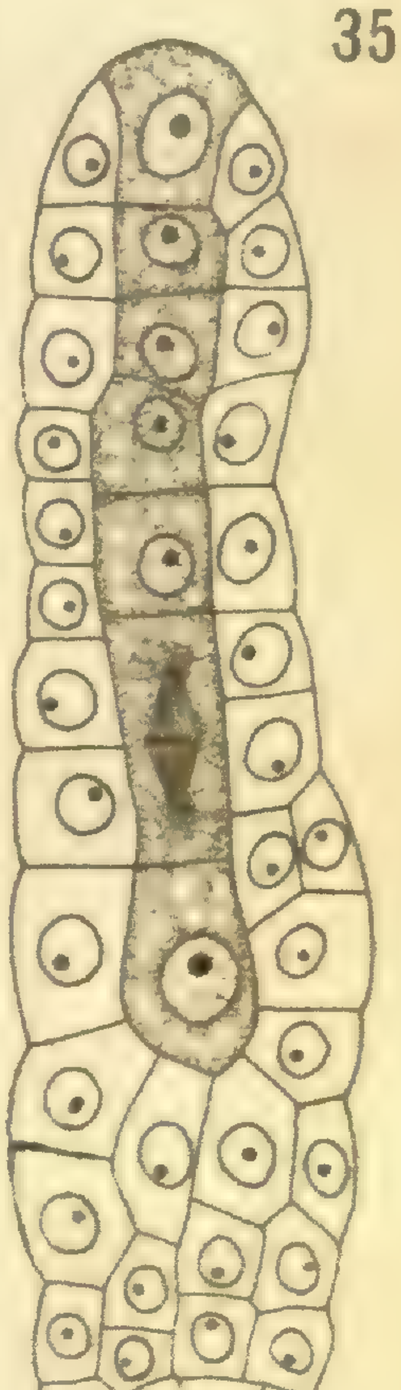

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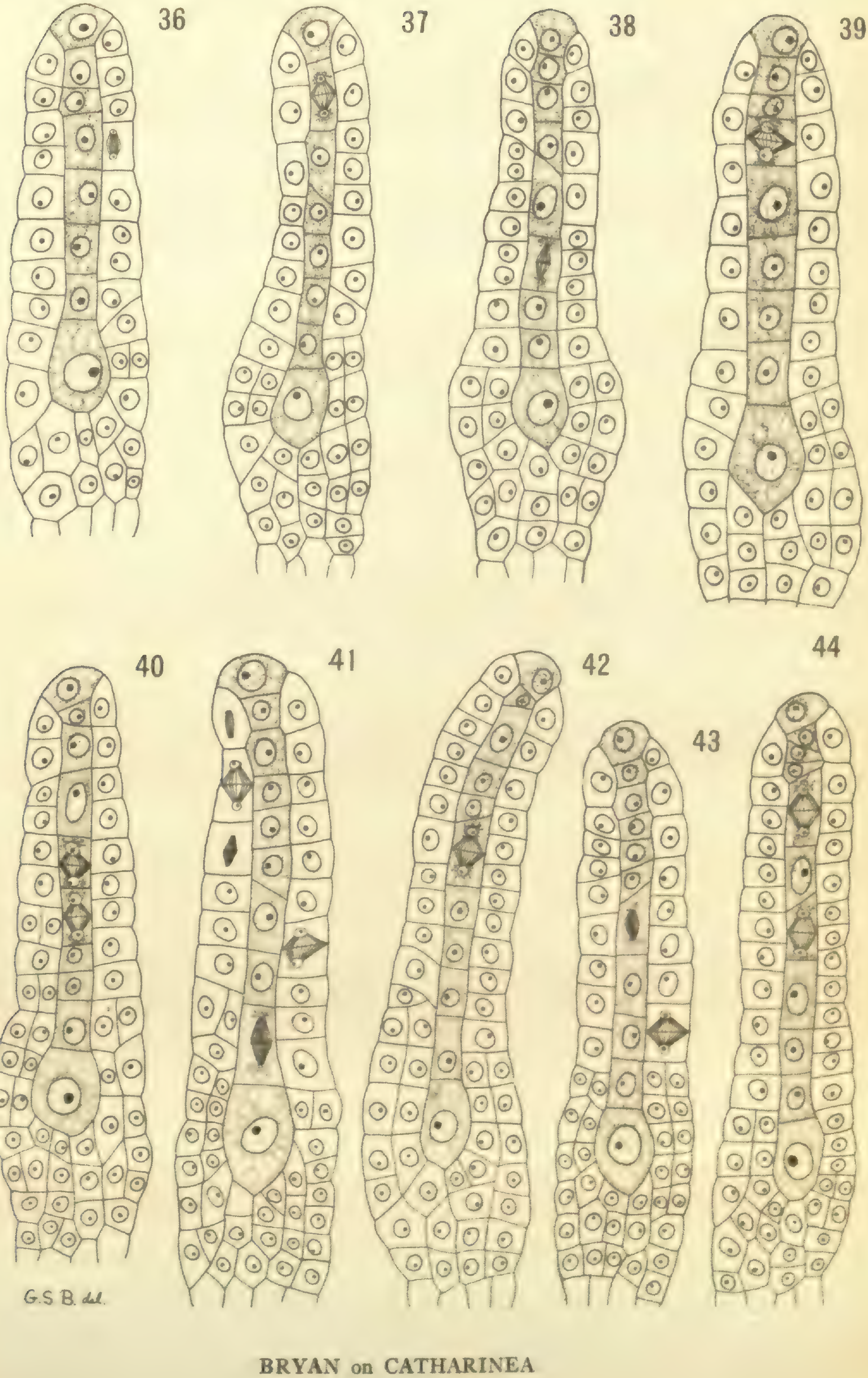

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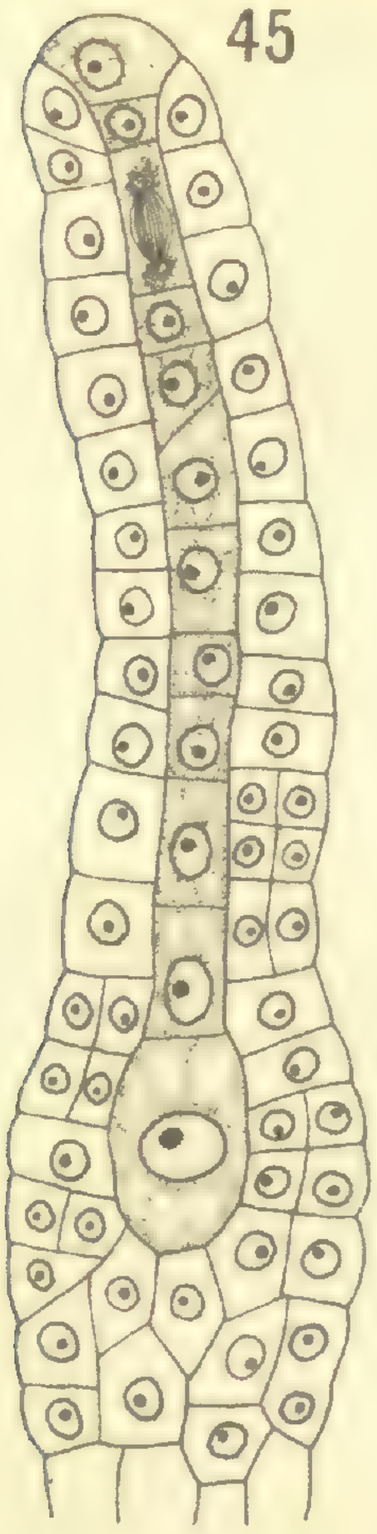
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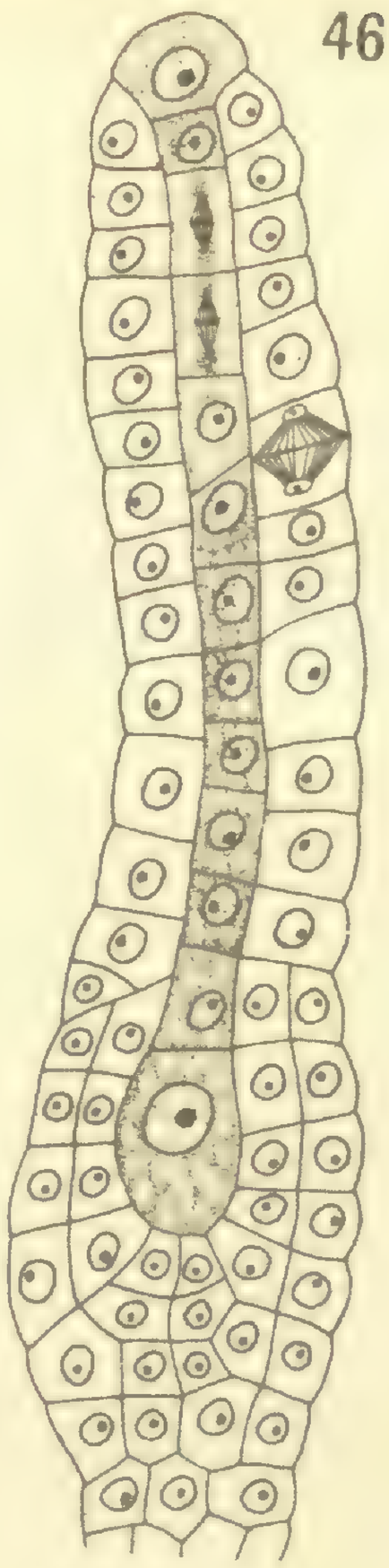
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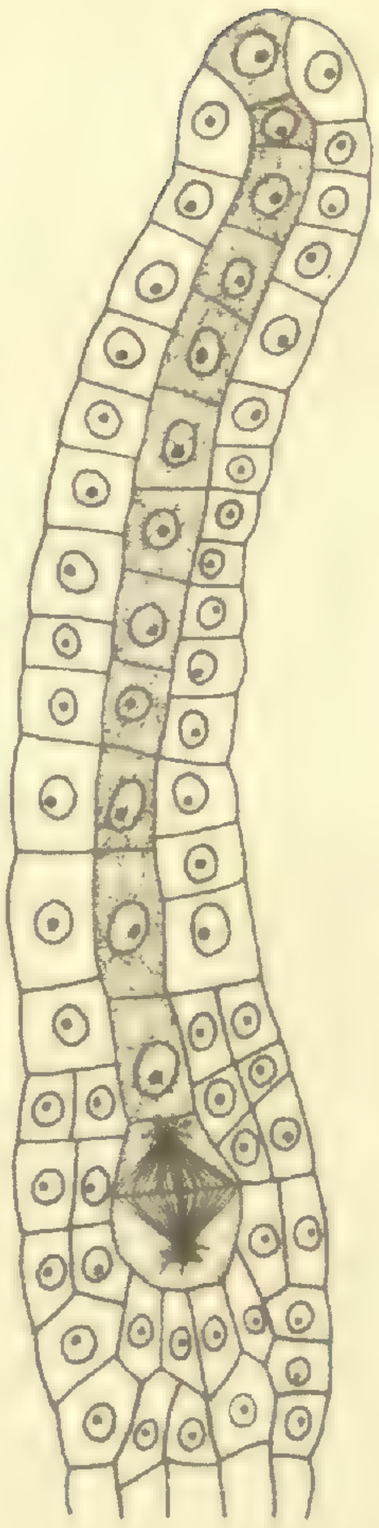
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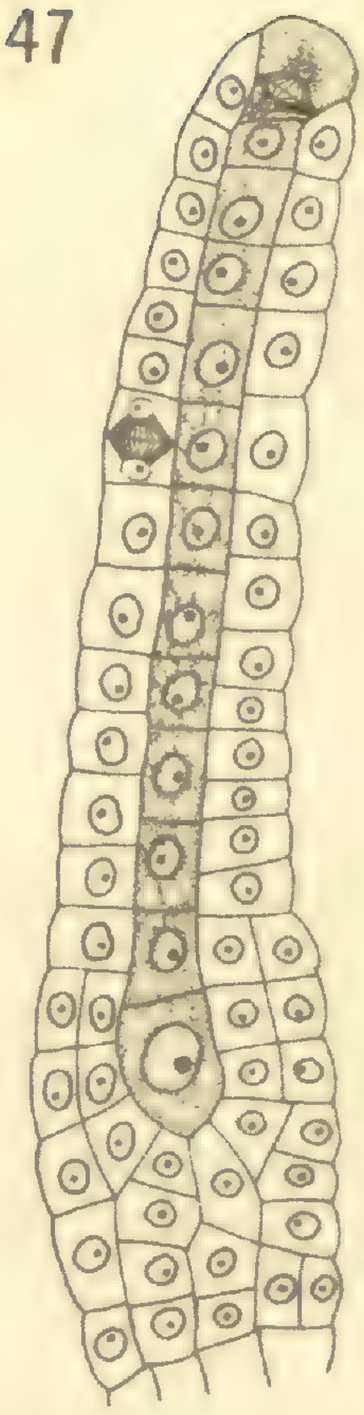
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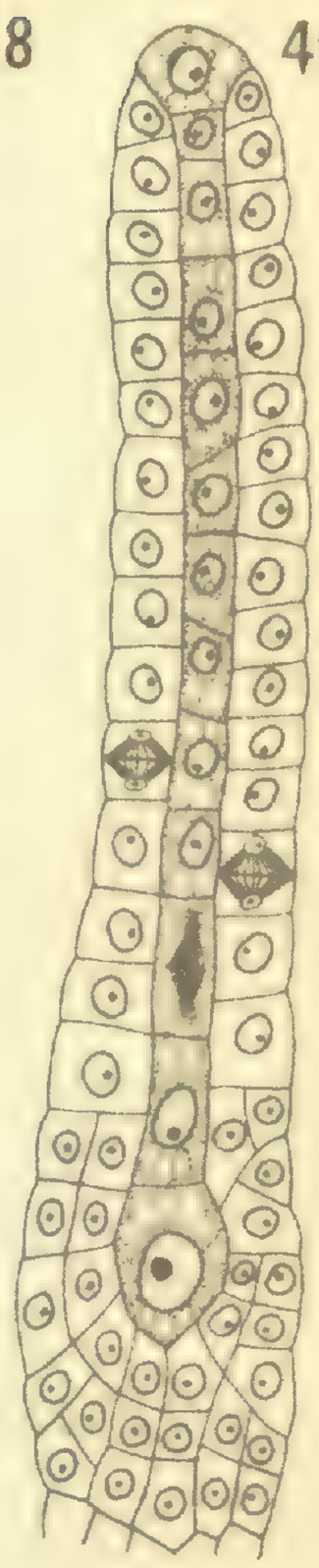
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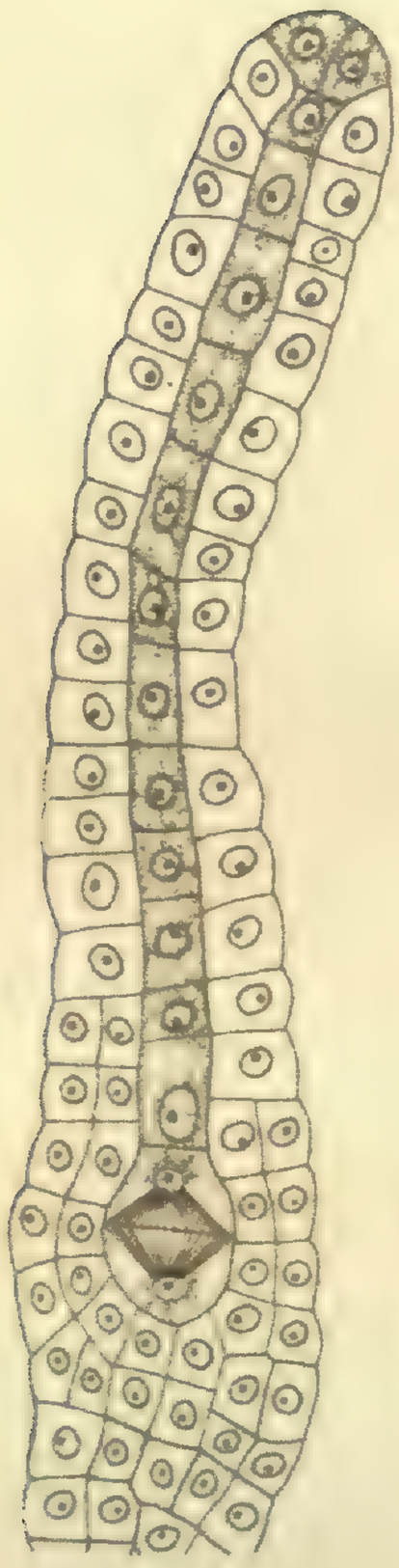
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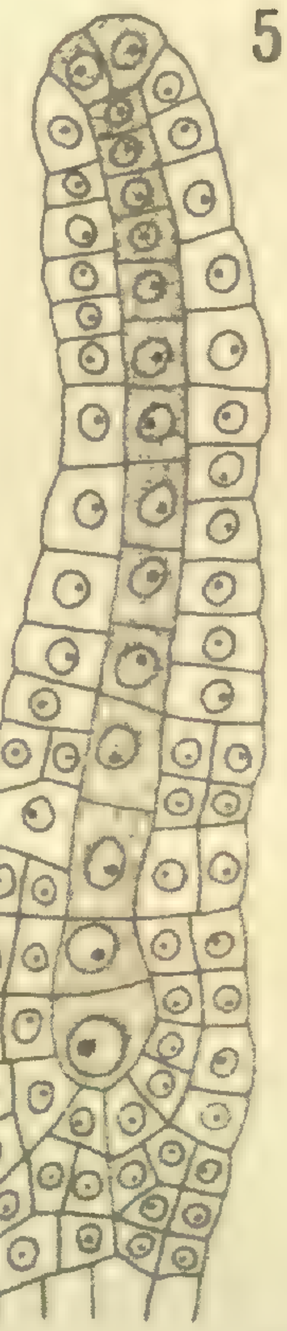
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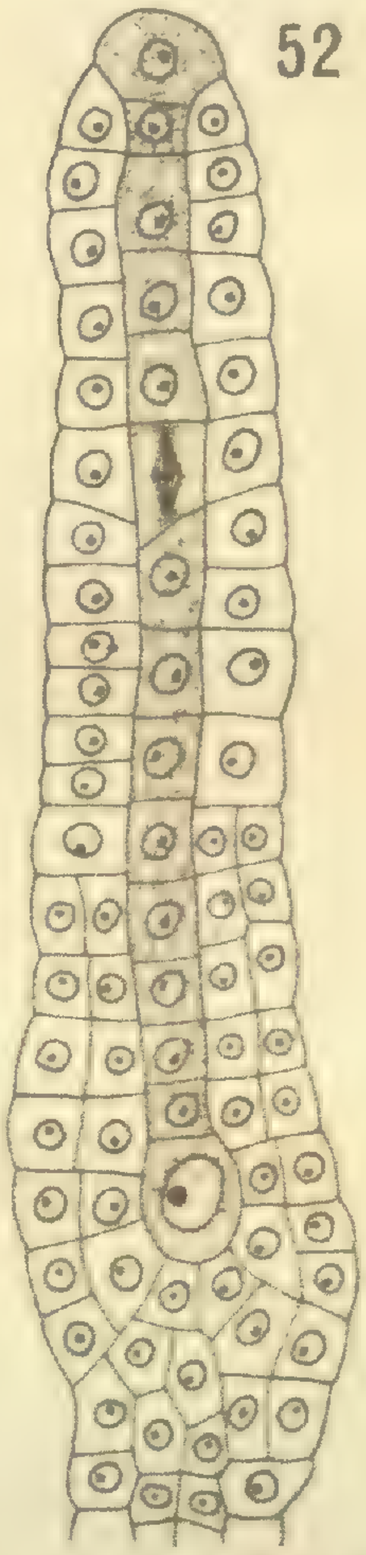
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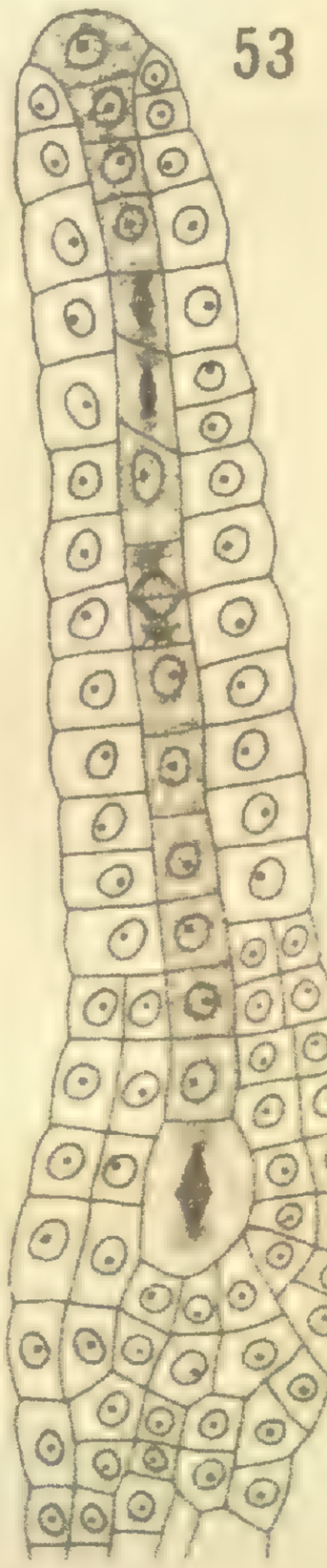
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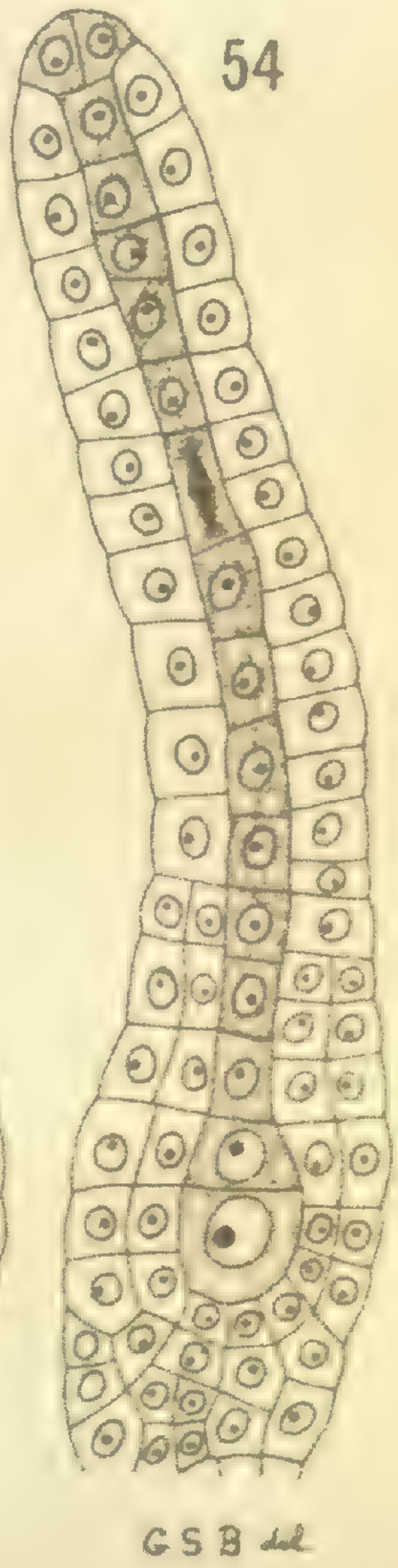
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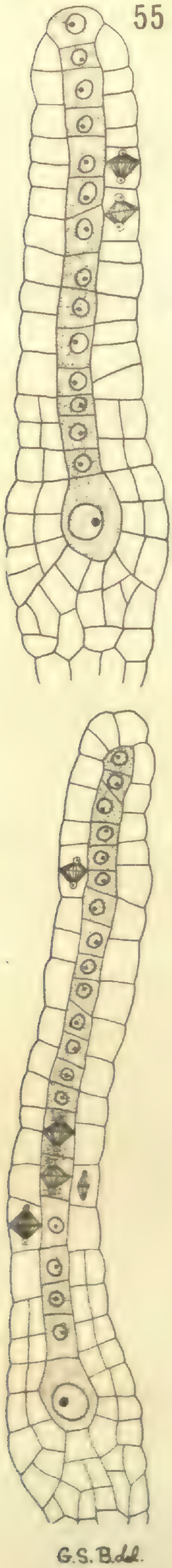
BRYAN on CATHARINEA



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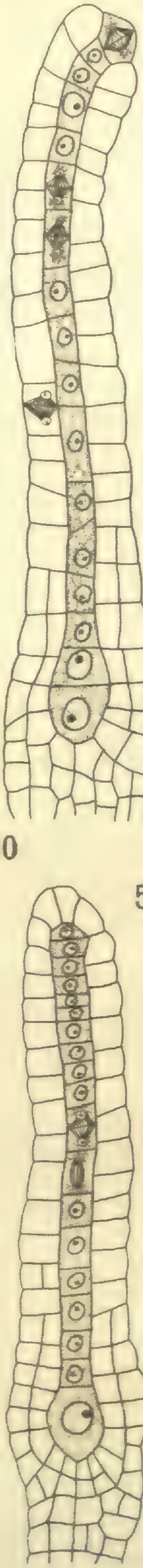

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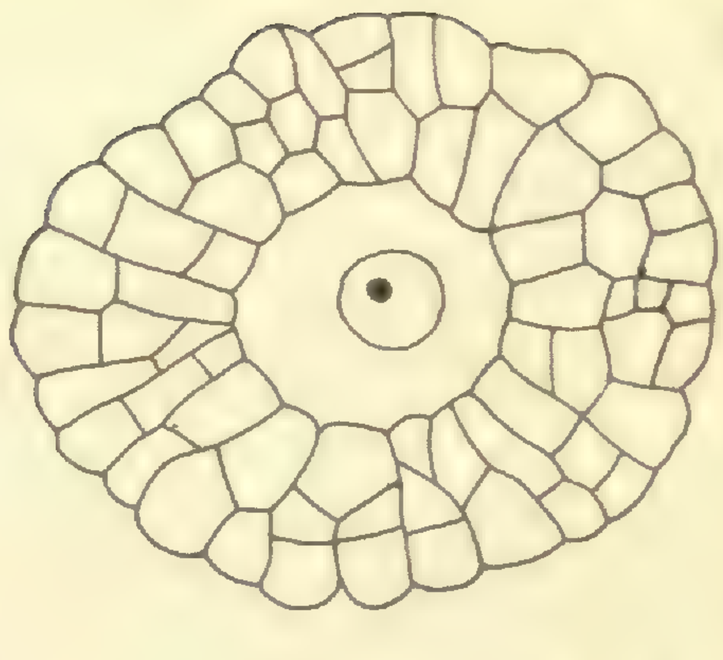

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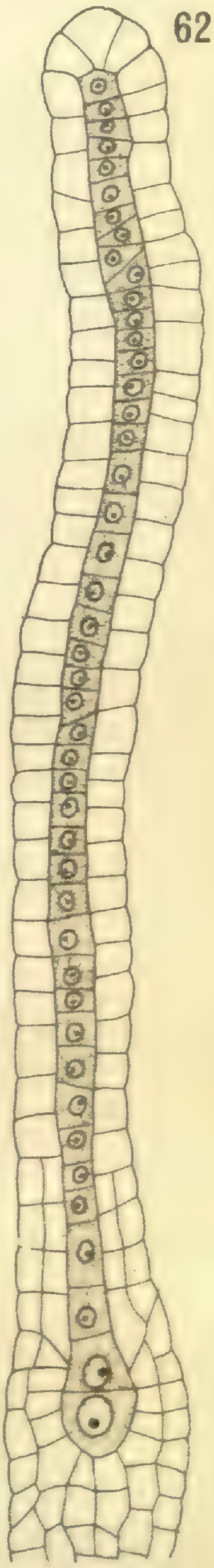

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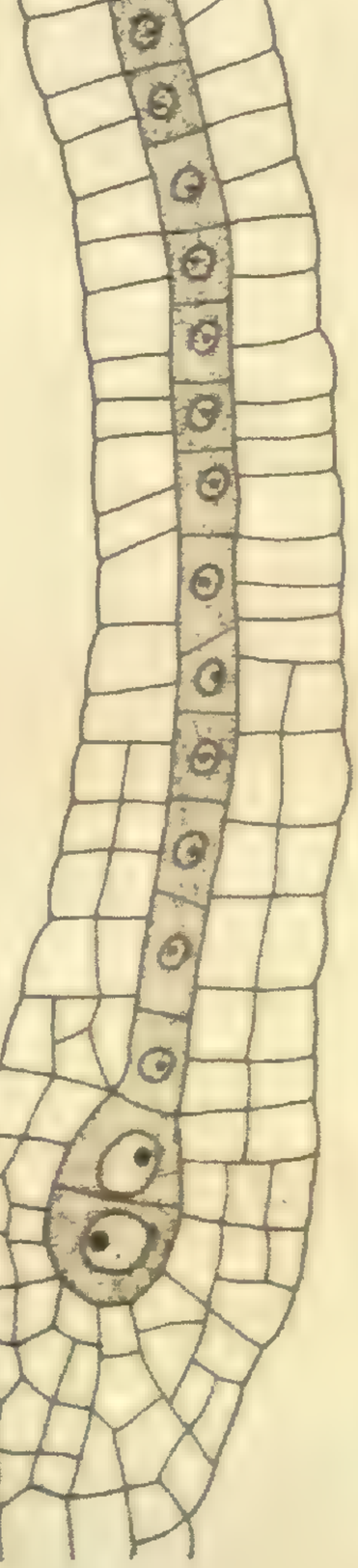

BRYAN on CATHARINEA

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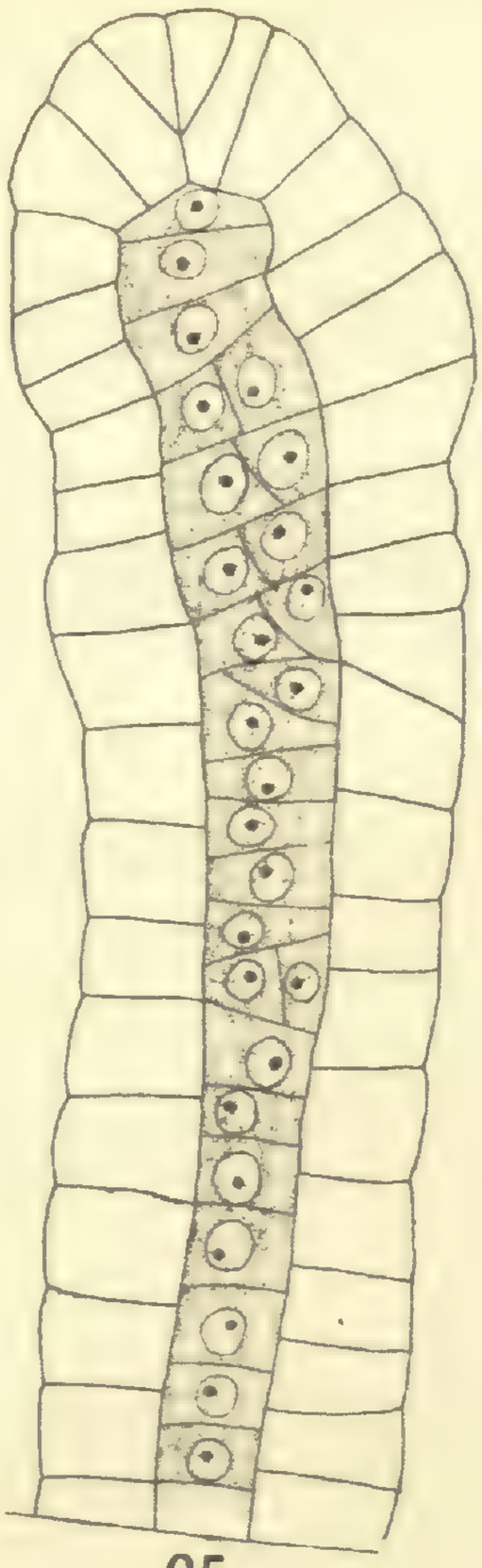

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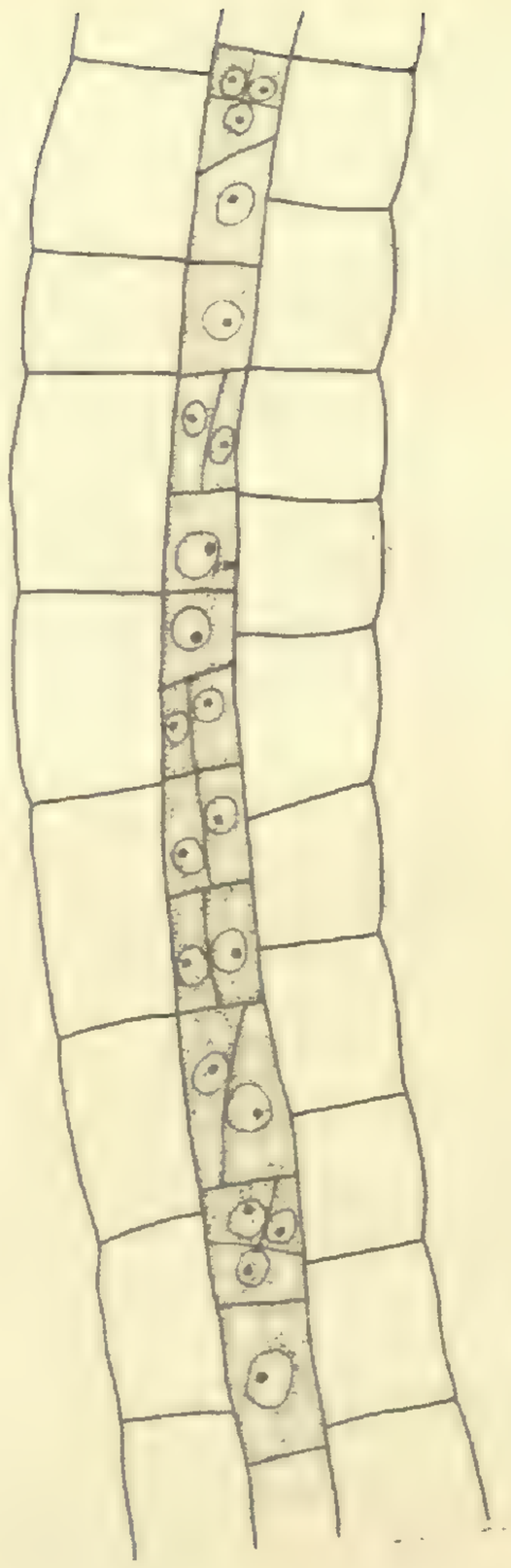

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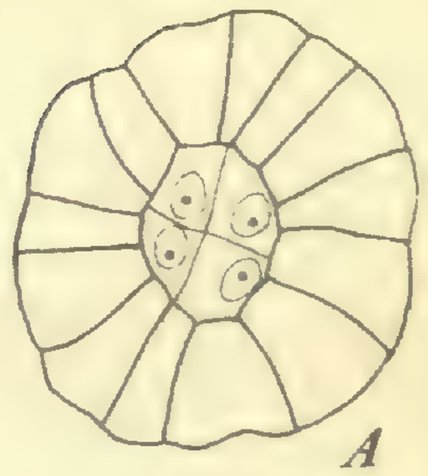

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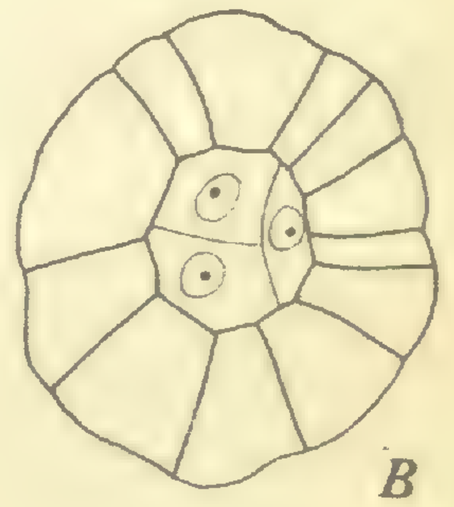

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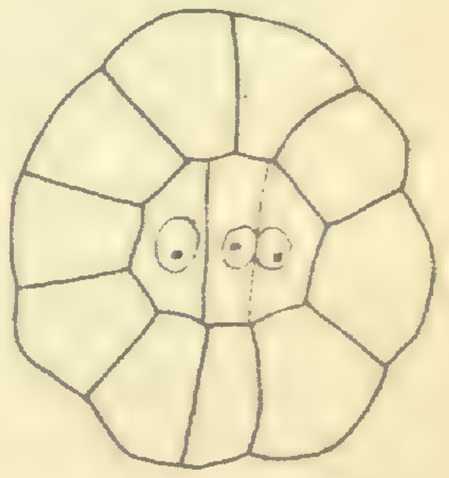

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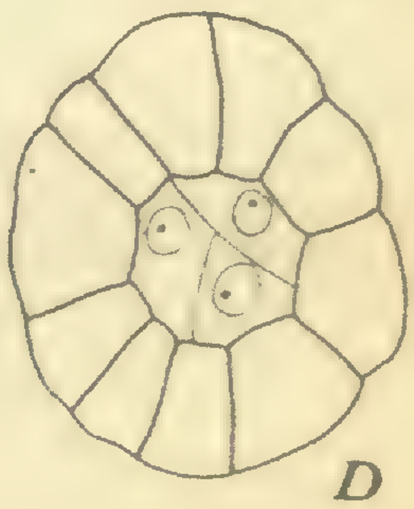

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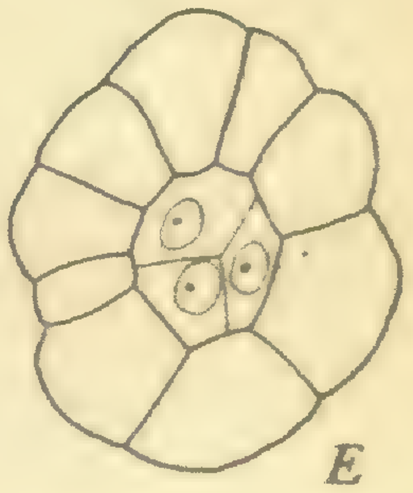

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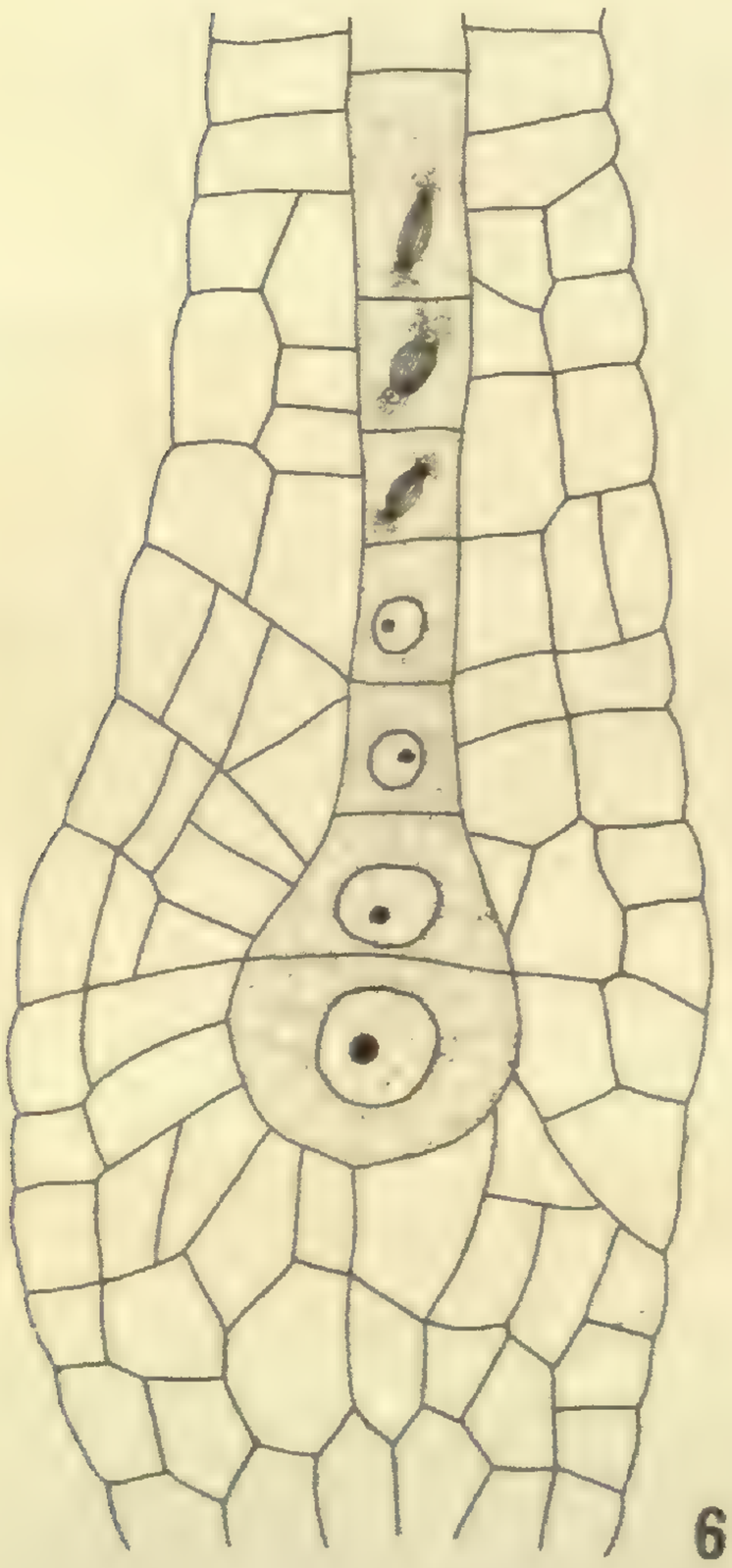

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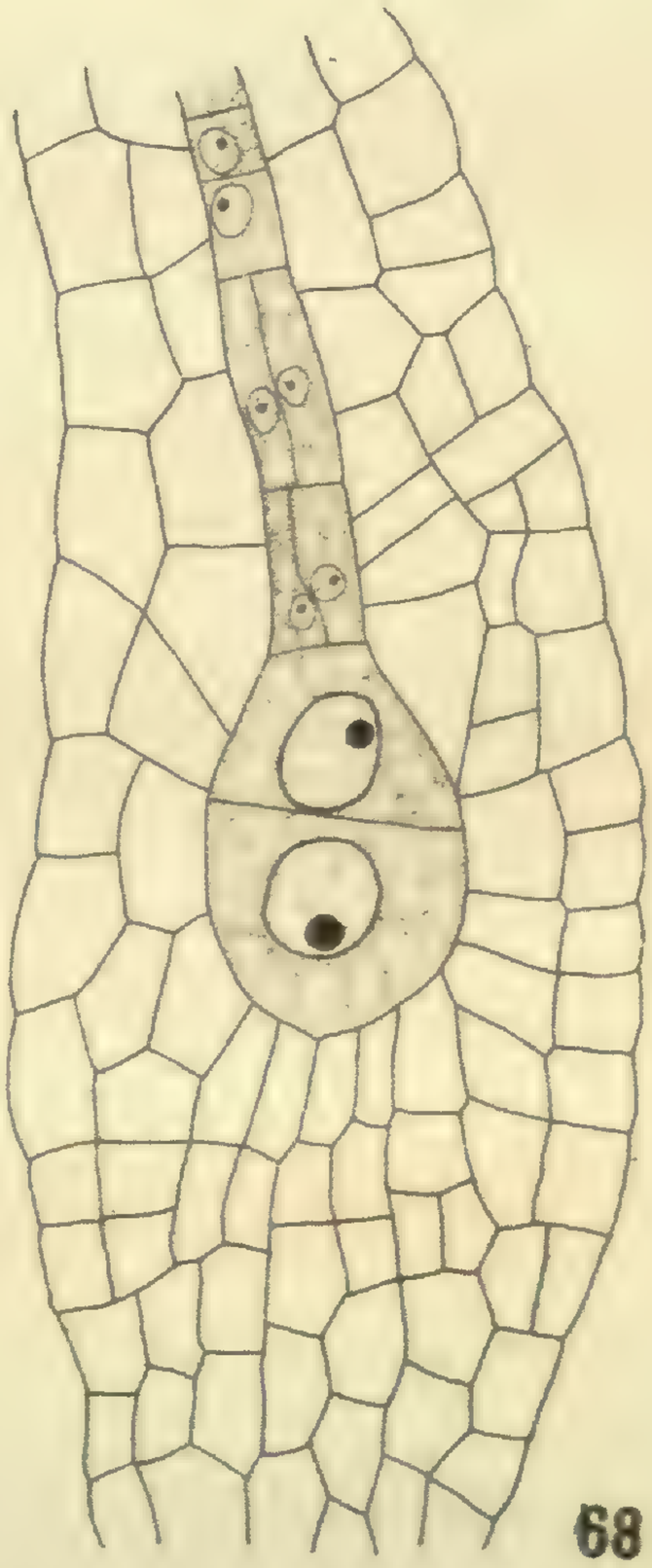

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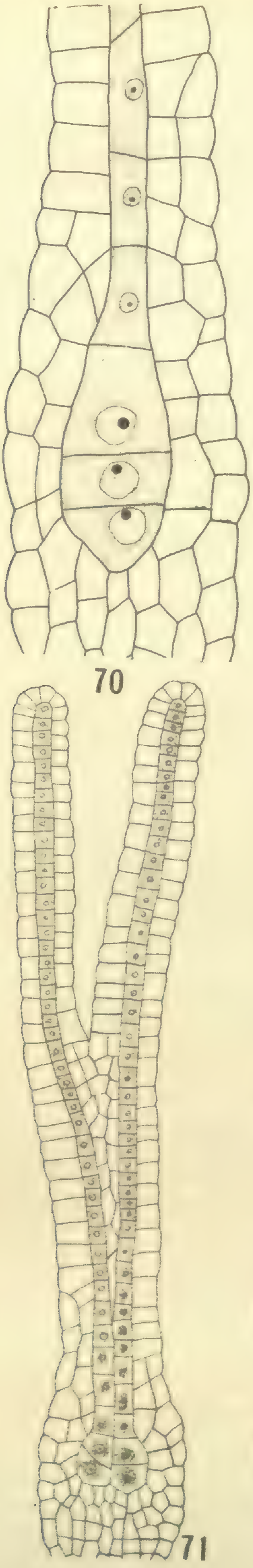
BRYAN on CATHARINEA



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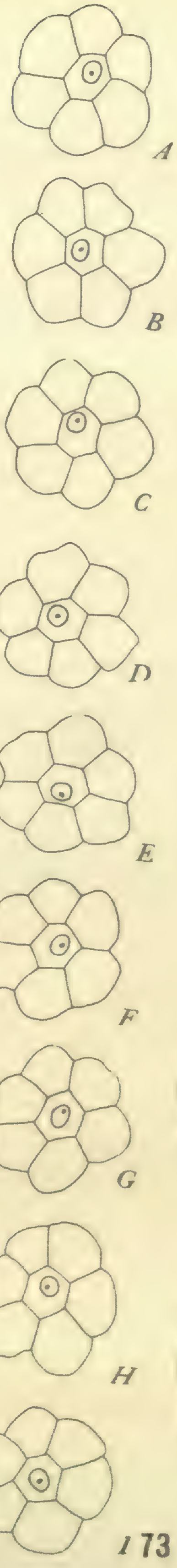

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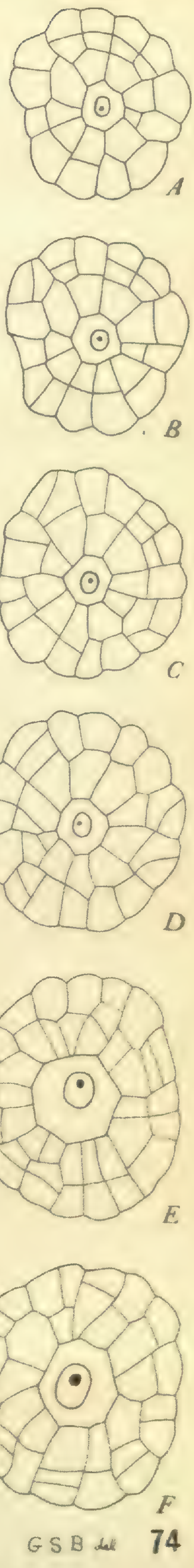

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BRYAN on CATHARINEA

STUDIES IN THE GENUS BIDENS. IV

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 232

EARL E. SHERFF

(WITH PLATES IX AND X)

Bidens mollifolia, sp. nov.—Herba annua, 1.2–1.8 m. alta (ex inscriptione Pringlei); caule et ramis plus minusve acute tetragonis, subviridibus aut purpurascentibus, dense tomentosis (aut supra etiam fere glabris); ramis ad finem liberum in aliquot ramulos aut pedunculos divisis, ut quaeque planta 30–60 capitula habeat. Folia opposita, petiolata, petiolo adjecto 2–9 cm. longa, ternata aut pinnata, dense et molliter pilosiuscula aut tomentosula, infra pallidiora; foliolis (3–7) ovatis aut lanceolatis, serratis, lateralibus (infimis interdum ternatis) 1–3.5 cm. longis et 0.5–2 cm. latis, terminali 1.8–5 cm. longo et 0.7–2.3 cm. lato; petiolis dense tomentosis, basi connatis, 0.3–2.5 cm. longis. Capitula breviter pedunculata pedunculis 0.5–3 cm. longis, ligulata, 5–7 mm. alta et ad anthesin et in fructu, ligulis adjectis 1.5–2 cm. lata. Involucrum basi hispidum, squamis duplici serie dispositis; exterioribus (6–8) linearibus, ad apicem obtusis, sparsim hispidis et plus minusve ciliatis, 2–3 mm. longis; interioribus lanceolatis, maximam partem glabris, margine diaphanis, 3–5 mm. longis. Ligulae (circ. 5) obovatae aut oblanceolatae, rosaceae, 3–7-striatae, apice 2–4-lobulatae lobulis subrotundis, 0.8–1 cm. longae. Paleae lineares, margine diaphanae, demum 5–7 mm. longae et terminis tortis achaenia superantes. Achaenia subtetragona, clavae simillima, infra angustiora, apici calva et areolata, nigra, glabra, 3–4 mm. longa.

C. G. Pringle 6050, at altitude of 2285 m., Sierra de San Felipe, Oaxaca, Mexico, November 16, 1894 (type in Herb. Gray); *E. W. Nelson* 1176 *pro parte*, at altitude of 2875–3353 m., in vicinity of Cerro San Felipe, Oaxaca, Mexico, September 1, 1894; *idem* 1363, at altitude of 2285–2875 m., 29 km., southwest of City of Oaxaca, Oaxaca, Mexico, September 10–20, 1894; *idem* 1476 *pro parte*, at altitude of 1675–2285 m., Valley of Oaxaca, Oaxaca, Mexico, September 20, 1894. All the specimens examined had been determined as

Bidens leucantha (L.) Willd. or *B. pilosa* L.; but in tall, slender habit, nature of pubescence, and short, clavate, exaristate character of fruit they are very distinct from either of these species.

Bidens cornuta, sp. nov.—Herba annua, 3–5 dm. alta; caule et ramis tetragonis, striatis, glabris, tenuibus. Folia opposita, petiolata, petiolo adjecto 3–12 cm. longa, 3–6 cm. lata, pinnata (aut summa bipinnata), ciliata, supra subglabra, infra sparsim adpresso-hispida; foliolis vel dentatis vel incisis vel etiam (imis foliorum superiorum) distincte partitis, ovatis aut lanceolatis; petiolis 0.3–3 cm. longis, glabris, ad basim hispidam connatis. Capitula terminalia, discoidea (aut interdum subligulata ?), tenuiter pedunculata pedunculis 2–9 cm. longis. Involucrum basi glabrum, squamis duplici serie dispositis; exterioribus (5–8) linearibus, glabris aut infra hispido-ciliatis, 2–3 mm. longis; interioribus late linearibus, glabris, striatis, margine diaphanis, 4–5 mm. longis. Paleae lineares, striatae, margine diaphanae, demum 5–10 mm. longae. Achaenia anguste linearia, striata, triaristata; maturis aristis longis (5–7 mm.) et divaricatis, supra tenuissime et retrorsum hamosis, demum plus minusve deciduis; quibusdam exteriorum achaeniorum subbadiis, hispidis, 6–10 mm. longis; interioribus elongato-attenuatis, nigris vel subnigris vel ad apicem subflavidis, infra glabris, supra hispidis, 1.3–2 cm. longis.

Dr. Edward Palmer 131, at altitude of 730 m., Hacienda San Miguel, southwestern Chihuahua, Mexico, August, 1885 (type in Herb. Gray).

ASA GRAY had treated this plant as "*Bidens bipinnata* L. var. aristis demum patentissimis"; but from *B. bipinnata* it differs decidedly in its less divided foliage, its narrower, more elongated, fewer-fruited heads, and its peculiar achenes with awns (when still attached) diverging so that, especially if pressed flat on the herbarium sheet, they suggest narrow horns. The specific description given above is drawn up from the type and various cotypes studied in different American herbaria. These vary considerably in the amount of dissection of the foliage, but all display very uniformly the peculiar fruit characters.

Bidens leptocephala, sp. nov.—Herba annua, 1–5 dm. alta, glabra, ramosa; caule et ramis tetragonis, striatis, tenuibus. Folia opposita (aut summa alternata), petiolata, petiolo adjecto 2–10 cm. longa, 1.5–5.5 cm. lata, bipinnata (inferiora non saepe unipinnata), minute ciliata, minutissime hispida (praecipue ad

venas); petiolis 0.3–4 cm. longis, sparsim hispido-ciliatis, ad basim connatis. Capitula terminalia, subradiata aut discoidea, ad anthesin 3–5 mm. alta et (radiis comprehensis) 4–8 mm. lata, in fructu 1–1.5 cm. alta et solum 2–4 mm. lata, tenuissime pedunculata, pedunculis 2–8 cm. longis. Involucrum basi subglabrum, squamis duplici serie dispositis; exterioribus (4–6) linearibus, ciliatis, 1–2.5 mm. longis; interioribus dimidio longioribus, lanceolatis, glabris aut ad apicem pubescentibus, margine diaphanis. Ligulae (si praesentes) circiter 3, minimae, circ. 2.5 mm. longae et 1.2 mm. latae, integrae aut ad apicem bidentes, 4–5-striatae, subalbidae. Paleae anguste lanceolatae, striatae, margine diaphanae, demum 5–7 mm. longae. Achaenia pauca (5–9 aut etiam 13), subtetragona, linearia, biaristata aristis retrorsum hamosis; quaedam exteriora badia aut subnigra, hispida, 6–8 mm. longa; interiora nigra aut ad apicem helvola, infra glabra, supra hispida, 0.9–1.4 cm. longa.

J. C. Blumer 1712, in shade, sandy alluvium soil at altitude of 1615 m., near Cedar Gulch, Paradise, Chiricahua Mountains, Arizona, September 21, 1907 (type in Herb. Gray); *idem* 2144, at altitude of 1760 m., base of rhyolite slope, Wilgus Ranch, Chiricahua Mountains, Arizona, September 4, 1907; *Dr. J. M. Bigelow* (Lieut. A. W. Whipple's Explor. Exped.), Hurrah Creek, Fort Smith to the Rio Grande, September 25, 1853–54; *E. L. Greene* 263, banks of the Upper Gila River, New Mexico, August 29, 1880; *J. G. Lemmon* 333, near Fort Huachuca, Arizona, in 1882; *idem*, Apache Pass, Chiricahua Mountains, Arizona; *idem* 3029, near Fort Huachuca, Arizona, in 1883; *Mr.* and *Mrs. J. G. Lemmon*, Apache Pass, Fort Bowie, Arizona, September 1881; *C. G. Pringle* 62, near Arivaca, Arizona, August 31, 1884; *David Griffiths* 1985, Hudson Ranch, near Pierce, Arizona, October 1900; *idem* 5994, fenced area, Santa Rita Forest Reserve, Arizona, September 27—October 4, 1903; *idem* 6014, above Range Reserve, Santa Rita Mountains, Arizona, September 12—October 18, 1903; *J. J. Thornber* 72, at altitude of 1780 m., Stone Cabin Canyon, Santa Rita Mountains, Arizona, September 14, 1903; *Griffiths* and *Thornber* 65, Santa Rita Mountains, Arizona, September 20—October 4, 1902.

This species has been confused with *Bidens Bigelovii* Gray and *B. bipinnata* L. by various botanists. Thus, for example, Asa Gray determined a specimen of *Bigelow's* 581 as *B. bipinnata*, but *Lemmon's* 3029, which was identical, he designated on the label as "*Bidens Bigelovii* varying toward *B. bipinnata*." From these two species it differs very clearly in its more slender, delicate habit, and in its slender fruiting heads with their smaller number of achenes. In foliage, some of the larger specimens have leaves rather like those of *B. Bigelovii*.

Bidens Langlassei, sp. nov.—Herba (annua?) erecta, circiter 1 m. alta, parce ramosa; caule glabro, acute et perspicuissime quadrangulato, basi tumido et ligneo. Folia opposita, petiolata, petiolo adjecto 2.5–5.5 cm. longa, pariter 2.5–5.5 cm. lata, bi- aut tripinnata (summa pinnata aut indivisa), supra glabra, margine hispidulo-ciliata, infra remotissime hispida, ultimis segmentis linearissimis, 0.5–1 mm. latis, integris, acute apiculatis; petiolis 3–7 mm. longis, plus minusve hispido-ciliatis, basi connatis. Capitula terminalia, ligulata, tenuiter pedunculata, pedunculis 1–11 cm. longis. Involucrum basi sparsim hispidum, squamis duplici serie dispositis; exterioribus (12–16) linearissimis, fere glabris, 6–7 mm. longis; interioribus linearibus, margine diaphanis, circ. 3 mm. longis. Ligulae (6–7) flavae, subanguste ellipticae, 7–15-striatae, ad apicem denticulatae, circ. 1.5 cm. longae. Paleae squamis interioribus similes sed demum longiores. Achaenia immatura. Ovaria (1–1.3 mm. longa) subplana, apice annulo 10–15 setulorum coronato.

E. Langlassé 332, in clay soil at altitude of 1200 m., "Le Faixin," southern Mexico (perhaps Farascon, Michoacan), September 8, 1898 (type in Herb. Gray).

The description is drawn from the type and one cotype (the latter in U.S. Nat. Herb.).

Bidens capillifolia, sp. nov.—Herba tenuis, verisimiliter annua, +3 dm. alta, ramosa, glabra (aut ramis ad eorum basim hispida); caule et ramis subteretis, striatis. Folia opposita, petiolata, petiolo adjecto 2–6 cm. longa, pinnata, foliolis linearis- simis, indivisis aut lobatis, margine integris, 0.5–1 mm. latis; petiolis 0.6–1.5 cm. longis, ad basim connatis. Capitula termi- nalia, discoidea, longe et tenuiter pedunculata, pedunculis 4–15 cm. longis. Involucrum basi plus minusve setoso-hispidum, squamis duplici serie dispositis; exterioribus (3–5) linearibus, glabris aut sparsim hispidis, 6–8 mm. longis; interioribus anguste lanceolatis, glabris aut sparsim hispidis, margine diaphanis, 4–6 mm. longis. Paleae lineares, margine diaphanae, demum 6–8 mm. longae. Achaenia linearia, tetragona, biaristata aristis retrorsum hamosis; 1–3 exteriora rufo-badia, sparsim tuberculato-hispida, circiter

6 mm. longa; interiora nigra (nisi ad apicem), elongata, glabra aut supra remote hispida, 9–14 mm. longa.

Barber and *Townsend*, Sierra Madre, Chihuahua, Mexico, July 17, 1899 (type in U.S. Nat. Herb., herb. no. 663169). The nearest known ally of this species is *Bidens tenuisecta* Gray, a plant with a less branched and less delicate habit, wider leaf divisions, and more hispid involucre. I have seen only the type specimen.

Bidens carpodonta, sp. nov.—Herba annua, erecta, 3–6 dm. alta; caule et ramis tetragonis, striatis, subglabris. Folia opposita, petiolata, petiolo adjecto 2–7 cm. longa, remotissime hispida, bi- aut tripinnata, ultimis segmentis linearibus, integris, 0.5–1.5 (raro 2.5) mm. latis, ad apicem acutis; petiolis ciliatis, basi connatis, 0.1–1.5 cm. longis. Capitula terminalia, ligulata, tenuiter pedunculata, pedunculis 3–10 cm. longis, ad anthesin ligulis adjectis 1.5–2.5 cm. lata et 0.6–1 cm. alta, in fructu 0.7–1 cm. lata et 0.8–1.2 cm. alta. Involucrum basi setoso-hispidum, squamis duplici serie dispositis; exterioribus (6–8) linearibus, hispido-ciliatis, indurato-apiculatis, 3–5 mm. longis; interioribus lanceolatis, margine diaphanis, glabris, paulo longioribus. Ligulae (circ. 5) flavae, ovatae, 12–15-striatae, apice 2–3-dentatae, 0.8–1 cm. longae. Paleae lineares, striatae, margine diaphanae, demum 5–8 mm. longae. Achaenia linearia, tetragona; quaedam exteriora subfusca, dense tuberculata, apice exaristato sed ad circumferentiam minute spinuloso-dentato, 4–6 mm. longa; interiora nigra, plerumque subsparsim tuberculato-hispida, demum elongata et 0.8–1 cm. longa, raro biaristata aristis nudis aut retrorsum 1–3-hamosis, sed plurimum exaristata, apice (erecte spinuloso-denticulato circulo) coronato.

Dr. Edward Palmer 419, San Lorenzo Canyon, 9.6 km. southeast of Saltillo, Coahuila, Mexico, September 21–23, 1904 (type in Herb. N.Y. Bot. Gard.).

Differs from *B. procera* Don in having achenes that are much more attenuate and lack elongate, numerously barbed aristae. From *B. Schaffneri* (Gray) Sherff it differs in general aspect of foliage and in its longer achenes. It is nearest to *B. ludens* Gray and might pass for that species except for its longer and much narrower achenes. A study of numerous specimens of *B. procera*, *B. Schaffneri*, and *B. ludens* has convinced me that these species, bearing at times a close superficial resemblance to each other and thus having been more or less confused in herbaria, are very definitely separable and have fruit

characters respectively constant. This being true, it seems certain that the 15 or more beautiful plants collected by *Palmer* (no. 419), and all of them having uniquely elongate, very attenuate achenes, are likewise specifically distinct.

Bidens pseudalausensis, sp. nov.—Herba, verisimiliter annua, circiter 6 dm. alta (ex Langlassei inscriptione), ramosa; caule et ramis tetragonis et acute angulatis, striatis, glabris. Folia opposita, petiolata, petiolo adjecto 2–7 cm. longa, 1–5.5 cm. lata, bipinnata, glabra; ultimis lobis cuneato-oblanceolatis, dentatis dentibus ad apicem induratis; petiolis 0.2–2 cm. longis, ad basim connatis, Capitula terminalia, tenuiter pedunculata pedunculis 1.5–6 cm. longis, ligulata, ad anthesin 6–7 mm. alta et (ligulis adjectis) circ. 1.5 cm. lata. Involucrum basi glabrum, squamis duplici serie dispositis; exterioribus (circ. 8) linearibus, ciliatis, 2–3 mm. longis; interioribus paulo longioribus, glabratis, margine diaphanis. Ligulae (circ. 5) albae (e Langlasseo), in sicco specimine luteolae, striatae, obovatae, ad apicem lobulatae aut obtusissime dentatae, 5–7 mm. longae. Achaenia (1–3 maturata in capitulis singulis) linearia, nigra, faciebus plus minusve glabra, marginibus tuberculato-hispida, biaristata (aristis sub apicem retrorsum hamosis), 7–9 mm. longa.—Differt a *B. alausensi* H.B.K. habitu ramoso, etc.

E. Langlassé 541, at altitude of 580 m., "El Ocote, Cerro Pedregoso, Michoacan and Guerrero," Mexico (type in U.S. Nat. Herb.).

Bidens aequisquama (Fernald), comb. nov.—*Bidens rosea* Schz. Bip. var. *aequisquama* Fernald, Proc. Amer. Acad. **43**:68. 1907.

This rare species differs very markedly from *Bidens rosea* Schz. Bip., not only in its involucres but also in its foliage and achenes. The type of *B. rosea* (*Cosmos pilosus* H.B.K.) is still extant (in Herb. Mus. Hist. Nat. Paris) and, though rather immature, is not separable from such specimens as *Heyde* and *Lux* 6172 and *Palmer* 192 (cf. GREENMAN, Proc. Amer. Acad. **41**: 264. 1905). From a study of numerous specimens that occur in different herbaria it is seen that *B. rosea* has a very slender, upwardly narrowed type of achenes, produced in rather small heads. Their aristae at maturity are mainly devoid of barbs. In some material (for example, *Heyde* and *Lux* 6164, Guatemala, 1894, a form with bipinnate leaves) the aristae are very short or even obsolete. But in *B. aequisquama* the achenes are in larger heads and are thicker. They are not narrowed above. Their aristae are much more

conspicuous, averaging $\frac{1}{3}$ to $\frac{1}{2}$ the length of the achene body, and are armed with many retrorse barbs that are not deciduous. Many other characters likewise are pronounced, making it seem best, therefore, to give herewith a full specific description, drawn from the type and various cotypes examined.

BIDENS AEQUISQUAMA, descript. amplificat.—Herba, +5 dm. alta; caule ramisque pubescentibus aut subglabris, quadrangularibus, striatis. Folia opposita, petiolata, petiolo adjecto 3–8.5 cm. longa, indivisa aut tripartita, ciliata, supra subglabra, infra sparsim adpresso-hispida et pallidiora; indivisis foliis lanceolatis, subcrasse serratis; foliolis foliorum tripartitorum similiter serratis, terminalibus ovatis aut lanceolatis, lateralibus ovatis et subsessilibus et minoribus; petiolis 0.4–1.8 cm. longis, hispidis, ad basim connatis. Capitula terminalia, ligulata, pedunculata, pedunculis 1–6 cm. longis et ad apicem creberrime albido-pubescentibus. Involucrum basi hispidum; squamis duplici serie dispositis; exterioribus (9–16) linearibus, hispidis, 2–4 mm. longis; interioribus subaequalibus, lanceolatis, glabris aut ad apicem et longitudinaliter medio hispidis, margine diaphanis. Ligulae (circ. 8) roseae, striatae, apice irregulariter 2–4-dentatae, 9–11 mm. longae, 6–8 mm. latae. Paleae lineares, margine diaphanae, 4–6 mm. longae. Achaenia nigra, linearia, ad apicem plus minusve hispida, biaristata, aristis non adjectis 4.5–7 mm. longa, flavis aristis retrorsum hamosis et 2.5–3 mm. longis.

"BIDENS SEEMANNII" Schz. Bip., ex Seem. Bot. Herald 307. 1852–57; *Cosmos Seemannii* Gray, Proc. Amer. Acad. **19**: 16. 1883.

SCHULTZ BIPONTINUS believed the genus *Cosmos* to be unworthy of separate treatment and accordingly he united it with *Bidens*. But since his time, special students of the Compositae have persisted very uniformly in recognizing *Cosmos* as a distinct genus (cf. GREENE, Pittonia **4**: 245. 1901). Indeed, the characters of the type species of that genus (*Cosmos bipinnatus* Cav.) are so pronounced as to make it very improbable that SCHULTZ BIPONTINUS' view will ever be accepted by botanists in the future. This being the case, there arises a slight difficulty in fixing upon the characters by which most accurately to distinguish between *Cosmos* and *Bidens*. The technical character most noticeable

in a number of *Cosmos* species is the rostrate achenes. *Cosmos bipinnatus* Cav., *C. parviflorus* H.B.K., *C. caudatus* H.B.K., *C. sulphureus* Cav., and *C. ocellatus* Greenm. are among those species displaying this character in a marked degree. A study of such species shows that the rostrate achenes are accompanied in *almost* every case by two other characters; namely, some shade of red in the ligules and the appearance of the interior involucre in the somewhat immature heads, suggesting the conspicuous inner involucre found so commonly in species of *Coreopsis*. But there are a few species of *Cosmos* in which the mature achenes tend to be erostrate. Thus, *Cosmos crithmifolius* H.B.K. and *C. linearifolius* (Schz. Bip.) Hemsl., in the many specimens that I have seen, fail almost uniformly to exhibit achenes swollen below and distinctly long-rostrate above as in *C. bipinnatus*. Yet in color of ligules and character of involucre they harmonize perfectly with *Cosmos*. While neither of these two characters is absolutely diagnostic, their simultaneous occurrence, coupled with a tendency of the central achenes at maturity to be elongate, even though indistinctly rostrate, shows both species to be true *Cosmos* beyond all question, and not *Bidens*.

HEMSLEY (Biol. Centr. Amer. **2**: 203. 1881), in dealing with the Compositae of Mexico, very correctly considered these two species as belonging to *Cosmos*. But "*Bidens Seemannii*," a species so identical *generically* with *Cosmos crithmifolius* that HEMSLEY himself erroneously referred to it *Parry* and *Palmer* 485 (true *C. crithmifolius*), he retained as *Bidens*. At a later date ASA GRAY suspected *Ghiesbreght* 264 of being "*Bidens Seemanii*" and stated that, if it was, the name should become *Cosmos Seemannii* (Proc. Amer. Acad. **19**: 16. 1883). In Gray Herbarium, the Ghiesbreght specimen studied by GRAY is still preserved in good condition. It is identical with *Seemann* 2014 (in Herb. Kew), thus confirming GRAY'S supposition. It is accompanied by a letter to GRAY from HEMSLEY, which must have been written later than 1881 and probably later than 1883 (the dates of the two works above cited). In this letter HEMSLEY, speaking of "*Bidens Seemannii*," wrote, "I do not see how *C. crithmifolius* differs generically."

GREENMAN (Proc. Amer. Acad. **41**: 265. 1905), relying upon the erostrate achenes, retained "*B. Seemannii*" in *Bidens*. But, as might be inferred already, if this treatment were to be adopted, then the subgeneric congeners of this species, such, for example, as *Cosmos crithmifolius*, would likewise have to be placed in *Bidens*, a procedure that surely would meet with little acceptance, if any. Thus it seems best to follow the views of GRAY and HEMSLEY in this matter and treat the species as *Cosmos Seemannii* (Schz. Bip.) Gray.

Besides the specimens of *C. Seemannii* listed by GREENMAN (*loc. cit.*), I have examined the following: *J. N. Rose* 3435, in the Sierra Madre, near Santa Teresa, Terr. de Tepic, Mexico, August 11, 1897; *Dr. Edward Palmer* 1852, Tepic, Terr. de Tepic, Mexico, January 5—February 6, 1892; *Arsène*, Cerro San Miguel, Morelia, Mexico, February 1909.

"BIDENS PALMERI" Gray, Proc. Amer. Acad. **22**: 429. 1887.

This species, with its strongly ribbed leaves, is very close to *Cosmos crithmifolius* H.B.K., but differs in its yellow rays and slightly different leaf outline. In most specimens the achenes are clearly erostrate, but occasionally some of the central achenes become highly elongated above, appearing almost distinctly rostrate and thus exactly simulating those of such species as *Cosmos crithmifolius* and *C. linearifolius*. This is especially notable in certain material collected by *Barnes* and *Land* (nos. 164 and 189, in Herb. Field Mus.). In fact, the subrostrate character of the achenes was known to GRAY (cf. GRAY, *loc. cit.*, "acheniis subulatis . . . subrostratis"). Yet, curiously enough, he placed this species in *Bidens*, while previously (Proc. Amer. Acad. **19**: 16. 1883) he had given the name *Cosmos Seemannii*, as shown above, to the Ghiesbreght plant, described by himself as having "essentially beakless . . . . achenes."

As this plant belongs very properly in *Cosmos*, it is renamed **Cosmos Landii**, nom. nov.[1]

I have examined the following specimens: *Dr. Edward Palmer* 315, Rio Blanco, Jalisco, Mexico, August 1886; *C. G. Pringle* 2348, vicinity of Guadalajara, Jalisco, Mexico, November 2, 1889; *idem* 11490, banks of ravines at

[1] In honor of Dr. W. J. G. LAND of the University of Chicago, the excellent specimens collected by him and C. R. BARNES having served materially to extend our conception of this species.

altitude of 1525 m., Rio Blanco near Guadalajara, Jalisco, Mexico, October 6, 1903; *C. R. Barnes* and *W. J. G. Land* 164 and 167, at altitude of 1707 m., Sierra de San Estaban, Jalisco, Mexico, September 28, 1908; *idem* 189, at altitude of 1737 m., Sierra de San Estaban, Jalisco, Mexico, September 28, 1908.

BIDENS TENUISECTA Gray, Plant. Fendl. 86. 1849; *Bidens cognata* Greene, Leafl. Bot. Crit. 1: 149. 1905.

In describing *Bidens cognata*, GREENE (*loc. cit.*) stated that it was "allied to *B. heterosperma*." He then proceeded to differentiate it from that species, which was very easy to do because *B. heterosperma* was so unlike it. Here, as in certain other cases (cf. SHERFF, BOT. GAZ. **56**: 494. 1913), GREENE'S error consisted in referring the plant to the wrong species and then founding a new species upon the points of dissimilarity. His type material (*O. B. Metcalfe* 1436) is merely a low, rather much branched form of *Bidens tenuisecta* Gray, with the type of which (in Herb. Gray) it is connected by numerous specimens in American herbaria.

"BIDENS DILLENIANA" Hill, Veg. Syst. **3**: 123. 1761.

This name seems to have escaped the serious attention of botanists for more than a century and a half. The *Index Kewensis*, although it cites the name, does not cite the habitat. HILL himself (*loc. cit.*) called it the "dwarf hemp agrimony" and stated that it was a British plant ("a petty plant of our own country"), but his generalized illustration and brief description were entirely too vague for satisfactory determination. However, on turning to his earlier work (Brit. Herb. 461. 1756), we find (under *Verbesina*) a much fuller description of the dwarf hemp agrimony, along with descriptions of what are now known as *Bidens cernua* L. and *B. tripartita* L. This description and the earlier name cited there by HILL, *Verbesina minima* Ray, show positively that the plants later named *Bidens Dilleniana* were merely the dwarf bog form of *Bidens tripartita* L. or the similar form of *B. cernua* L. (or very likely both these forms without distinction).

The name *Dilleniana* was given evidently for the very reason that DILLENIUS (Cat. Plant. Giss. 167, App. 66. 1719; ex Ray, Syn. 188. *pl. 7. fig. 2.* 1724) was the one to introduce the name *Verbesina minima* which HILL sought to displace.

BIDENS TRIPARTITA L. Sp. Plant. 831. 1753.

DRUCE (Fl. Berks. 283. 1897) has treated the dwarf form of this species as "forma *minima*." But it should be noted that DRUCE is not the first author to adopt this status, LARSSON (Fl. Werml. 221. 1859) having used it long before. Similarly, the dwarf form of *B. cernua* L., named "forma *minima*" by DRUCE (Herb. Dillen. 67. 1907), evidently under the impression that such treatment was new, was already described, years before, as *B. cernua* f. *minima* (Larss., *loc. cit.*, 220).

BIDENS CERNUA L. Sp. Plant. 832. 1753; *Bidens Kelloggii* Greene, Pittonia 4: 267. 1901.

A careful study of the type and other cited specimens of *Bidens Kelloggii* (in U.S. Nat. Herb.) shows them to be incapable of separation from *B. cernua*. GREENE classed these forms among the segregates from *B. laevis* (L.) B.S.P., but most inconsistently so, for, at the same time, he even stated that "DR. TORREY . . . . more correctly referred them to *B. cernua*."

It may be remarked in passing that, in the future, supposedly new species allied with *Bidens cernua* should be described only after taking the utmost care to see that they are not mere atypic forms of that species. It would be interesting to subject *B. cernua* to elaborate breeding experiments. A beginning in this direction has been made already by GUPPY (Studies in Seeds and Fruits 480. 1912).

BIDENS ALBA DC. Prodr. 5: 605. 1836.—*Coreopsis alba* L., Sp. Plant. 908. 1753; *Chrysanthemum americanum, ciceris folio* . . . . Herm. Par. 124. *pl. 124.* 1698; *Bidens pilosa* L. var. *alba* O. E. Schulz (*excl. synon. maximam partem*), Urb. Symb. Antill. 7: 136. 1911; *Bidens dondiaefolia* Less. (ex descript. et loci situ), Linnaea 5: 155. 1830.

This peculiar plant was treated by DECANDOLLE as one of the "species non satis notae." LINNAEUS' description ("foliis subternatis cuneatis serratis") and citation of habitat ("Insula St. Crucis") were drawn directly from the work of HERMANN, the Paradisus Batavus. Reference to this work (*loc. cit.*) shows a plant very unique in habit, especially as to its many foliose, sterile shoots and its cuneate leaf divisions. So rare has this form been in herbaria that it is easy to understand DECANDOLLE'S misgivings

regarding it. Recently, however, there has come to hand (in Herb. Field Mus.) a specimen (*C. R. Orcutt* 2886, Vera Cruz, Mexico) which agrees most minutely and strikingly with Hermann's plate which LINNAEUS cited; also another (*idem* 2991, Sanborn, Vera Cruz, Mexico) agreeing satisfactorily but having proliferous heads. Coming from the same locality in Mexico are other specimens which show transitions to a more elongate type of plant with some 5-parted leaves. One of these (*Mueller* 148, in Herb. N.Y. Bot. Gard.) is labeled *Bidens dondiaefolia* Less., a species likewise from Vera Cruz and the description of which it fits very well (I have not yet seen LESSING's type). It is noteworthy that LESSING called attention to the sterile shoots of this species; "rami plures steriles."

From these facts it is evident that *B. dondiaefolia* Less. is a synonym for *B. alba* (L.) DC., and that *B. alba* is a local species native mainly to the state of Vera Cruz, Mexico. It possibly does not occur in St. Croix, as stated by HERMANN (*loc. cit.*). Dr. C. F. MILLSPAUGH, himself an authority upon the flora of St. Croix, suggests to me, and very plausibly so, that in the preparation of HERMANN's posthumous work, the name "Sancta Crux" perhaps became substituted for "Vera Crux," and that thus the locality "Insula St. Crucis" finally was published.

As to the worthiness of *Bidens leucantha* (L.) Willd. to rank separately from *B. alba*, future field observations and breeding tests are highly desirable. It seems much the safer course to retain the two names separately for the present rather than merge them as done by O. E. SCHULZ (*loc. cit.*).

The plant collected by *Ghiesbreght* (no. 551) and referred by GRAY (Proc. Amer. Acad. **19**: 16. 1883) to *B. dondiaefolia* is a very different plant and is typical *B. chiapensis* Brandeg. The following list represents the specimens of *B. alba* so far determined by myself at the Field Museum and the New York Botanical Garden (certain numbers appearing to accompany mixed material elsewhere).

Fred Mueller 148, Vera Cruz, Mexico, August 1853; *idem* 4067, Orizaba, Vera Cruz, Mexico (in 1855?); *J. M. Greenman* 6, near wharf, City of Vera Cruz, Vera Cruz Mexico, January 22, 1906; *idem* 23, La Laguna, near City

of Vera Cruz, Vera Cruz, Mexico, January 22, 1906; *idem* 97, along the shore, north of City of Vera Cruz, Vera Cruz, Mexico, January 24, 1906; *C. R. Orcutt* 2886, Vera Cruz, Mexico, February 16, 1910; *idem* 2991, Sanborn, Vera Cruz, Mexico, April 18, 1910.

BIDENS HUMILIS H.B.K., Nov. Gen. et Sp. **4**: 234. 1820.—*Bidens consolidaefolia* Turcz., Bull. Soc. Nat. Mosc. **24**: 185. 1851.

TURCZANINOW (*loc. cit.*) based his species *Bidens consolidaefolia* upon *Jameson* 693 from Quito. At Gray Herbarium is one sheet of specimens by JAMESON "from the vicinity of Quito and elsewhere," and the specimens at the top of the sheet, while lacking a number, match precisely the description of *B. consolidaefolia*. It is seen from a study of many specimens of *B. humilis* collected in the last half century, that *B. consolidaefolia* is merely a slender-leaved form of *B. humilis* and is in no way specifically distinct.

BIDENS CONNATA Muhl. ex Willd., Sp. Plant. **3**: 1718. 1804.

FERNALD (Rhodora **10**: 197. 1908) has given an excellent discussion of this species. Commonly it occurs with simple leaves and then is the var. *petiolata* (Nutt.) Farwell, but occasionally it possesses tripartite leaves, matching MUHLENBERG's original description of the species proper. In July 1913 it was my good fortune to be invited to accompany Dr. FERNALD from Cambridge, Mass., to Winchester, Mass., and there observe the tripartite leaves of the typical form, which grows in good quantity at that place. Tripartite leaves were present on young plants less than 3 dm. high. In the Central United States, however, tripartite leaves seem absent except on large, robust, well-developed specimens. FERNALD (*loc. cit.*) gives the range for the typical, tripartite-leaved form as extending from "Quebec to Massachusetts and Michigan and doubtless southward." This range is seen to be extended westward by the following specimens:

C. W. Duesner, Miller, Indiana, in 1908; *O. E. Lansing Jr.* 727, Roby, Indiana, September 16, 1899; *idem* 1179, Lake, Indiana, September 22, 1900; *idem* 2641, Roby, Indiana, September 20, 1906; *E. E. Sherff* 2016, Elgin, Illinois, September 12, 1915; *Dr. J. T. Stewart*, Peoria County, Illinois; *F. W. Johnson* 1123, Three Lakes, Wisconsin, August 24, 1914; *J. H. Schuette*, Green Bay, Wisconsin, August 30, 1881, and September 10, 1882; *idem*, Brown County, Wisconsin; *F. H. Burglehaus*, near Minneapolis, Minnesota, September 1892.

BIDENS FRONDOSA L. var. ANOMALA Porter ex Fernald, Rhodora 5: 91. 1903.

This variety is peculiar in having upwardly barbed awns, but the precise significance of their occurrence is difficult at present to judge. In a specimen of the corresponding form of *B. connata* Muhl., the var. *anomala* Farwell, I have observed numerous downwardly barbed awns in the same heads with upwardly barbed awns (*Vasey*, near Georgetown, Washington, D.C., September 23, 1888, in U.S. Nat. Herb.). WIEGAND (Bull. Torr. Bot. Club **26:** 415. 1899) cites also similar material collected at Ithaca, New York. FERNALD (Rhodora **15:** 75. 1913) inclines toward regarding *B. frondosa* var. *anomala* as a geographic variety. He cites Pennsylvania, New Jersey, Delaware, also the region from Maine to Cape Breton Island for its distribution. It is interesting to note that out of many hundreds of specimens of *B. frondosa* that I have examined from Europe and America, there were observed only two instances of specimens of the var. *anomala* having been collected outside the range given by FERNALD. These plants, coming from Kansas and Nebraska, go further in showing the distribution to be very discontinuous.

E. Hall, Kansas, in 1869 (in U.S. Nat. Herb.); *P. A. Rydberg* 1707, Middle Loup River, near Thedford, Nebraska, August 26, 1893 (in Herb. Gray, etc.).

BIDENS ANGUSTISSIMA H.B.K., Nov. Gen. et Sp. **4:** 233. 1820.

The type of *B. angustissima* is matched very well by SCHULTZ BIPONTINUS' type of *B. linifolia* (both in Herb. Mus. Hist. Nat. Paris), except that the latter has only simple leaves, while the former has tripartite leaves. KLATT, in publishing the description of *B. linifolia* (Flora **68:** 203. 1885), described the heads as discoid. But that rays were present on at least the Paris material is shown by SCHULTZ BIPONTINUS' label, in his own handwriting, which reads, "achs. rad. calva . . . ." Furthermore, PRINGLE (no. 6924, granitic ledges at altitude of 2895 m., Cerro Ventoso above Pachuca, Hidalgo, Mexico, August 18, 1898) has collected many fine specimens of the simple-leaved form, and these all show orange-yellow rays, about 8 on each head. Thus the only difference to be found between the two species is the questionable one of foliage.

At Gray Herbarium there occurs a single sheet (*Coulter* 375, Mexico) with three slender but well-developed specimens; the largest one, at the left, matching the type of *B. angustissima*, and the other two, at the right, matching the type of *B. linifolia*. From these it appears safe to say that *B. linifolia* will be found, on future field study, to be merely a simple-leaved state of *B. angustissima*.

BIDENS REFRACTA Brandeg., Zoe 1: 310. 1890.—*Bidens riparia* H.B.K. var. *refracta* O. E. Schulz, Urb. Symb. Antill. 7: 132. 1911.

SCHULZ (*loc. cit.*) regarded this species as only a variety of *B. riparia* H.B.K., and he differentiates the two forms on the basis of fruit characters. But an examination of many specimens of each form shows that the only genuine difference is in the foliage. *B. refracta* has tripartite leaves, while *B. riparia* has bipinnate leaves. This difference SCHULZ seems to have overlooked. Indeed, he even refers to *B. refracta* a plant collected by *Tonduz* (no. 13618, several fine specimens of which are in U.S. Nat. Herb., Herb. Brit. Mus., etc.) that is identical in foliage and other parts with the type and *Bonpland* cotype of *B. riparia* (in Herb. Mus. Hist. Nat. Paris).

Of 22 collections of *B. refracta* studied so far, I have seen only one instance where the leaves were not of the tripartite kind. In this case (*Jenman* 5499, British Guiana, October 1889, in U.S. Nat. Herb.) the leaves are somewhat more divided, but still far from resembling those of true *B. riparia*. The probabilities are strong that *B. refracta* and *B. riparia* are entirely distinct species.

BIDENS SQUARROSA H.B.K., Nov. Gen. et Spec. 4: 238. 1820.—*Bidens tereticaulis* DC., Prodr. 5: 598. 1836; *Bidens antiguensis* Coult., BOT. GAZ. 16: 100. 1891; *Bidens tereticaulis* DC. var. *antiguensis* O. E. Schulz, Urb. Symb. Antill. 7: 142. 1911; *Bidens tereticaulis* DC. var. *sordida* Greenm., Proc. Amer. Acad. 39: 115. 1903; *Bidens tereticaulis* DC. var *indivisa* Robins., Proc. Bost. Soc. Nat. Hist. 31: 270. 1904; *Bidens Coreopsidis* DC. var. *procumbens* Donn. Sm., BOT. GAZ. 42: 299. 1906.

DECANDOLLE (*loc. cit.*), in describing his *Bidens tereticaulis*, stated that it differed in having glabrate leaves, all of which were

trisected, in having heads smaller, and in coming from a different region ("Differt a *B. squarrosa* foliis glabriusculis . . . . capitulo minore, foliis etiam superis trisectis et patria"). But he had not seen the type material of *B. squarrosa*, as is evidenced by his failure to use the abbreviation "v.s." in connection with its description (*loc. cit.*, 599). At Paris (in Herb. Mus. Hist. Nat. Paris) is still preserved KUNTH's type of *B. squarrosa*. Upon the label are the words "*Bidens squarrosa* mihi . . . . Caracas." This is positively the specimen KUNTH had at hand in drawing up his description. It consists of a branchlet coming from a portion of a stem. The eaves of the branchlet are simple, as described by KUNTH. One well preserved leaf, still attached,[1] and certain similar but more fragmentary leaves, some of them broken loose, remain with the stem proper. These leaves are very important, as they establish definitely and beyond all question the identity of *B. squarrosa* with pubescent forms of *B. tereticaulis* DC., and not with *B. reptans* (L.) G. Don (with which it is equated by O. E. Schulz, *loc. cit.*, 140). This will become evident on reference to pl. IX, drawn directly from the type with the utmost fidelity to all details.

The presence of pubescence in this species is not of specific importance, a fact recognized by GREENMAN (*loc. cit.*) and by SCHULZ (*loc. cit.*, 142) when they treated very tomentose specimens as mere varieties of *B. tereticaulis*. Nor is the presence of several or even many undivided leaves of decisive value, a fact recognized by ROBINSON (*loc. cit.*) in treating as a variety of *B. tereticaulis* a specimen with all of its leaves simple. That COULTER (*loc. cit.*) treated his *B. antiguensis* (pl. X) as a distinct species[2] is easily explained by the fact that the strong superficial resemblance of his first type specimen's foliage to that of certain hispid forms of *B. leucantha* (L.) Willd., led him to contrast it with that species,

[1] At least when I examined it in 1914, as may be verified by a photograph taken by myself at that time and now deposited, with many hundreds of others of the genus *Bidens*, in the herbarium of Field Museum. The specimen was very brittle and certain parts were observed to crack even during my cautious handling of it.

[2] It may be noted that the Guatemalan form *B. antiguensis* has glabrous awns on its achenes. This character, which, however, is inconstant in some cases, is noticeable in nearly all the specimens of *B. squarrosa* from Central America. In South America and in Mexico the awns are almost always barbed.

from which he very properly regarded it as distinct. It is interesting to observe that COULTER also noted the remarkable variation in pubescence ("exceedingly variable in pubescence, from glabrous to pilose-pubescent").

B. Coreopsidis DC. var. *procumbens* Donn. Sm. is a form of this species. Its leaves are mainly 5-parted and are slightly narrower than in most specimens. It approaches rather closely *B. reptans* (L.) G. Don var. *bipartita* O. E. Schulz, of Porto Rico, but as a rule is quite distinct from that form.

Since *B. squarrosa* thus is found to be so highly variable, it is thought best to present here a rather full and representative list of specimens studied: *H. H. Rusby* 1642, at altitude of 609 m., Guanai, Bolivia, May 1886; Mig. Bang 1406, Guanai-Tipuani, Bolivia, April to June 1892; *Humboldt* and *Bonpland*, Caracas, Venezuela; *A. Fendler* 696, near Tovar, Venezuela, 1854–55; *H. H. Smith* 519, at altitude of 609 m., Jiracasaca, Santa Marta, Colombia, October 1898–1901; *C. Hoffmann* 383, Valley of the Rio Legardo, Costa Rica; *Ad. Tonduz* 12284, at altitude of 1800 m., forests of the Mala Via at Copey, Costa Rica, April 1898; *idem* 7265, banks of the Rio Maria Aguilar near San Jose, Costa Rica, December 29, 1892; *idem* 13600, in thickets, Nicoya, Costa Rica, January 1900; *idem* 7058, at altitude of 1100 m., San Francisco de Guadalupe, Prov. San Jose, Costa Rica, January 1896; *idem* 7248, in thickets upon banks of the Rio Torres near San Francisco de Guadalupe, Costa Rica, January 4, 1893; *Biolley* 7028, in copses near San Mateo, Costa Rica, January 18, 1892; *C. F. Baker* 2121, Dept. Leon, Nicaragua, January 17, 1903; *idem* 2214, Masaya, Dept. Masaya, Nicaragua, January 27, 1903; *H. Pittier* 1838, at altitude of 600 m., in hedges around Copan, Honduras, January 9, 1907; *Luis V. Velasco* 8873, San Salvador, Salvador, December 1905; *W. A. Kellerman* 5341, El Rancho, Sierro de las Minas Mountains, Baja Vera Paz, Guatemala, January 6, 1906; *idem* 5351, at altitude of 1205 m., Moran, Amatitlan, Guatemala, February 11, 1905; *idem* 6118, Volcano Acatenango, Chimaltenango, Guatemala, February 8, 1907; *idem* 8035, at altitude of 1067 m., El Rancho, Sierra de las Minas Mountains, Baja Vera Paz, Guatemala, January 1908; *Maxon* and *Hay* 3162, at altitude of about 550 m., vicinity of Secanquim, Alta Vera Paz, Guatemala, January 4, 1905; *John Donnell Smith* 2354, at altitude of 1778 m., Antigua, Sacatepequez, Guatemala, April 1890; *Heyde* and *Lux* 4193, at altitude of 1956 m., Buena Vista, Santa Rosa, Guatemala, December 1892; *E. W. D. Holway* 4, at altitude of 1778 m., Guatemala City, Dept. Guatemala, Guatemala, December 31, 1914; *idem* 110, at altitude of about 1778 m., Solola, Guatemala, January 25, 1915; *H. von Tuerckheim* 297, at altitude of 1565 m., Coban, Alta Vera Paz, Guatemala, May 1886; *idem* 7900, at altitude of 350 m., Cubilquite, Alta Vera Paz, Guatemala, January 1901; *Charles C. Deam* 109, at altitude of 49 m., Los Amates, Izabal, Guatemala,

February 12, 1905; *Enrique Th. Heyde* 666, Guatemala, in 1892; *Berlandier* 730 and 2150, Tantoyuca, Vera Cruz, Mexico, December 1830; *idem* 2148, Mexico; *Botteri* 489, Orizaba, Vera Cruz, Mexico; *Bourgeau* 1560, Valley of Cordoba, Vera Cruz, Mexico, October 12, 1865; *idem* 3093, Orizaba, Mexico, October 3, 1866; *C. Conzatti* 122, at altitude of 1200 m., Mountains of Oaxaca, Mexico, September 20, 1895; *idem* 1581, at altitude of 1800 m., Cerro San Antonio, Oaxaca, Mexico, October 28, 1906; *idem* 2269, at altitude of 2000 m., Cerro San Felipe (Distr. del Centro), Oaxaca, Mexico, October 18, 1908; *Conzatti* and *Gonzalez* 1133, at altitude of 850 m., Cordoba, Vera Cruz, Mexico, December 1900; *E. A. Goldman* 30, at altitude of 244 m., near Metlaltoyuca, Puebla, Mexico, January 27, 1898; *idem* 493, Apazote, Campeche, Mexico, December 28, 1900; *E. W. D. Holway* 3667, Oaxaca, Mexico, October 18, 1899; *E. Langlassé* 689, at altitude of 300 m., southern Mexico, December 2, 1898; *E. W. Nelson* 1508, at altitude of 1585–2075 m., Valley of Oaxaca, Oaxaca, Mexico, October 2, 1894; *idem* 1824, at altitude of 1600–1955 m., 9.6 km. above Dominguillo, Oaxaca, Mexico, October 30, 1894; *idem* 3410, near Yajalon, Chiapas, Mexico, November 21, 1895; *C. R. Orcutt* 3031, Sanborn, Vera Cruz, Mexico, April 18, 1910; *C. A. Purpus* 3633, Zacuapan, Vera Cruz, Mexico, October 1909; *Charles L. Smith* 298 and 633, at altitude of 1955–2135 m., Monte Alban, near City of Oaxaca, Oaxaca, Mexico, October 1894; *idem* 587, Coatzacoalcos, Vera Cruz, Mexico, February 6, 1895; *Lucius C. Smith*, at altitude of 2135 m., Rancho de Calderon, Oaxaca, Mexico, September 10, 1894.

Bidens Brandegeei, sp. nov.—Herba annua, erecta (nisi infra plus minusve arcuata), 3–5 dm. alta, maximam partem albido-hispida. Caulis quadrangulatus, striatus, ramis tenuibus ramosus. Folia opposita, petiolata, petiolo adjecto 1–8 cm. longa, pinnata aut bipinnata, supra minus albido-hispida; foliolis 3–5, ovatis (aut ovato-lanceolatis) serratisque et non dissimilibus iis *B. leucanthae* (L.) Willd., aut pinnati partitis, lobulis aut dentibus indurato-apiculatis; petiolis 0.2–2.5 cm. longis, basi connatis. Capitula pauca, terminalia, ligulata, tenuiter pedunculata, pedunculis monocephalicis, 3–8 cm. longis. Involucri squamis subaequalibus duplici serie dispositis; exterioribus (circ. 8) linearibus, 1-nervatis, apiculatis, albido-ciliatis et-hispidis, 4–5 mm. longis; interioribus lanceolatis, membranaceis, glabratis aut pubescentibus, margine diaphanis. Ligulae (circ. 5) obovatae, in specimine sicco albido-flavae, 7–9-striatae, ad apicem obscure dentatae, 1–1.3 cm. longae. Paleae lineares, margine diaphanae, 3–4 mm. longae. Achaenia (submatura) attenuato-linearia, striata, exaristata, supra antrorsum hispida, 4–6 mm. longa.

T. S. Brandegee, in vicinity of San Luis Tultitlanapa, Puebla, near the Oaxaca boundary line, Mexico, in 1908 (first type sheet in Herb. Univ. Cal., herb. no. 134267, and second type sheet, dated July, also in Herb. Univ. Cal., herb. no. 134268); *C. A. Purpus* 4429 (in vicinity of San Luis Tultitlanapa, Puebla), Oaxaca, Mexico, August 1908.

A species having at times all the leaves tripartite and then deceivingly like *B. leucantha* (L.) Willd. except as to achenes. The description is drawn mainly from the two flowering specimens on the first type sheet, but the achene characters are described from the single fruiting head present on the second type sheet. The species is here named for T. S. BRANDEGEE, who himself has described several species of *Bidens*, and who by his collections and writings has extended our knowledge of this genus to a considerable extent.

Recently, Dr. SIDNEY F. BLAKE has sent from Gray Herbarium a specimen of *Bidens* that appeared to him as allied with *Bidens rubifolia* H.B.K., but none the less new. The plant was collected by HOLWAY in Guatemala early in the present year, and is described by him as "climbing over trees 40–50 feet and then dropping down nearly to the ground." Its heads, in antithesis, measure about 6 cm. in diameter. From *B. rubifolia* it may easily be recognized in herbarium specimens by its large involucre and the unique characters of the involucral bracts. A detailed description is presented here:

Bidens Holwayi Sherff and Blake, sp. nov.—Herba scandens, caule demum 20–30 m. longo, ascendente (ex HOLWAYO) in altitudinem 12–15 m.; ramis tetragonis, glabris, striatis. Folia opposita, petiolata, petiolo adjecto 6–18 cm. longa, tripartita aut summa indivisa, ciliata, supra glabrata (nisi ad venas), infra plus minusve piloso-hispida, serrata; foliolis lateralibus ovatis aut ovato-lanceolatis, terminali ovato-lanceolato aut lanceolato. Petioli 1.5–4cm. longi, basi connati et hispido-ciliati. Capitula magna, ligulata, pedunculata pedunculis (in uno specimine observato) 12–13 cm. longis. Involucrum ad basim dense piloso–tomentosum, squamis longis duplici serie dispositis; exterioribus 8 (aut 9) late linearibus, hispido-ciliatis, subsparsim hispidis, 9–15 mm. longis; interioribus, saepe paulo brevioribus, anguste lanceolatis, ad faciem exteriorem piloso-tomentosis, marginibus diaphanis. Ligulae (5, aut interdum verisimiliter etiam 6 aut 7) lineari-ellipticae, flavae, 9–11-striatae, 2.3–3 cm. longae, ad apicem irregulariter 2–4-dentatae aut-lobulatae. Paleae lineares, demum 1.2–1.5 cm. longae, marginibus

diaphanis. Achaenia linearia, subplana, nigra, ciliata, ad facies sparsim hispida, ± 1.3 cm. longa, ad apicem nonnullis erectis setis coronata, biaristata aristis retrorsum hamosis et divaricantibus.

E. W. D. Holway 816, Quezaltenango, Guatemala, January 31, 1917 (type in Herb. Gray).

BIDENS SAMBUCIFOLIA Cav. Icon et Descript. 3:15. *pl. 229.* 1794; *Bidens alamosana* Rose, Contrib. U.S. Nat. Herb. 1:104 *pl. 6.* 1891.

A comparison of the type illustration of *Bidens alamosana* with that of *B. sambucifolia* reveals a remarkable similarity. Furthermore, the descriptions of the two species are very close and differ materially only in that the ligules of *B. sambucifolia* are described as scarlet; those of *B. alamosana* are yellow or orange-yellow.

CAVANILLES' description was based upon material from the Royal Garden at Madrid and which was stated by him to have come originally from Peru and Mexico. It may well be that his citation of Peru was entirely erroneous, as I have never been able to find a specimen from elsewhere than Mexico. An examination of numerous specimens collected in Mexico shows the ligules to be usually yellow or orange-yellow, but in certain rare cases the ligules (in the dried specimens) have a color so reddish as to explain quite plausibly how Cavanilles was led to call them scarlet ("corolla . . . . coccinea"). Thus, for example, a specimen by *T. S. Brandegee*, collected at Culiacan, Sinaloa, Mexico, September 12, 1904 (in Herb. Univ. California), has one flowering head with a distinct reddish shade to its orange ligules. The other two flowering heads present on the same sheet have yellow-orange ligules. Clearly, CAVANILLES and ROSE were dealing with the same species, and the name *Bidens sambucifolia*, antedating *B. alamosana* by nearly a century, must be used hereafter for this species.

UNIVERSITY OF CHICAGO

SHERFF on BIDENS

SHERFF on BIDENS

EXPLANATION OF PLATES IX AND X

PLATE IX

Bidens squarrosa H.B.K.: *a*, fruiting spray ×0.75; *b*, exterior bract ×3; *c*, interior bract ×3; *d*, ligulate floret ×3; *e*, palea ×4.5; *f*, disk floret ×4.5; *g*, achene ×4.5; all from type in Herb. Mus. Hist. Nat. Paris.

PLATE X

Bidens squarrosa H.B.K. (*B. antiguensis* Coult.): *a*, portion of branch ×0.7; a^1 and *k*, small portions of 2 plants showing comparative pubescence ×0.7; *b* and *l*, exterior bracts ×4; *c* and *m*, interior bracts ×4; *d* and *n*, ligulate florets ×4; *e*, palea ×4; *f* and *o*, disk florets ×4; *g*, anthers ×35; *h*, pollen grain ×1000; *i*, style branches ×20; *j*, achene ×6; *a-j* from first type sheet and *k-o* from second type sheet of *Bidens antiguensis* (both *J. D. Smith* 2354 in Herb. Univ. Chicago).

EFFECT OF SOME ALKALI SALTS UPON FIRE-HOLDING CAPACITY OF TOBACCO

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 233

HENRY R. KRAYBILL

Introduction

Of all the qualities which are essential in a good cigar tobacco no single one is quite so important as the burn. The general composition of the leaf and the salts which it contains exert a great influence upon the course of the combustion. It is a well established fact that chlorides tend to prevent complete combustion and thereby products are formed which are injurious to the flavor and aroma. On the other hand, the carbonates of the alkalies, particularly of potassium, aid the combustion and increase the fire-holding capacity.

The term "burning qualities" with reference to a cigar is general and includes many points. The most important of these points are evenness of burn, color of ash, firmness and coherence of the ash, and the fire-holding capacity. The fire-holding capacity refers to the length of time the leaf or cigar will continue to glow after ignition. A cigar tobacco must have primarily a good fire-holding capacity, and for this reason this has been the main criterion in judging the burn of cigar tobacco.

Historical

It was maintained early that the fire-holding capacity depended upon the content of nitrates. SCHLOSING (15) and later others have disproved this theory. SCHLOSING (15), NESSLER (12, 13), KISSLING (8), and VAN BEMMELN (17) have shown that in a good burning sample of tobacco potassium is present in excess of the amount equivalent to combine with the sulphuric and hydrochloric acids, while in a poor burning sample it is equal to this amount or less. This indicates that potassium salts of organic acids favor a good burn. GARNER (4) concludes that the fire-holding capacity is

dependent primarily upon the content of potassium combined with organic acids.

NESSLER (12) concluded that potassium sulphate exerts a favorable influence upon the burn; while JENKINS (6) found that fertilizing with potassium sulphate increased the content of sulphuric acid in the tobacco so that in some cases it injured the burn. GARNER (4) concluded that sulphates in general are injurious to the burning qualities, but not to so great an extent when all of the sulphuric acid is combined with the potash; while PATTERSON (14) found no apparent relation of the content of sulphuric acid to the burn.

NESSLER (12, 13), KISSLING (7), BEHRENS (2), VAN BEMMELN (17), BARTH (1), PATTERSON (14), CARPENTER (3), and GARNER (4) agree that chlorides are injurious to the burn. KISSLING (8) considered the content of ash to have little influence upon the burning qualities; while PATTERSON (14) and CARPENTER (3) concluded that a high content of ash was conducive to a good burn. NESSLER (12) found that calcium and magnesium have little effect except to whiten the ash. KISSLING (7) found good burning samples of tobacco high in content of calcium and fairly high in magnesium. GARNER (4) concluded that calcium in general does not greatly affect the fire-holding capacity, but is essential in the production of a good ash, and that large amounts of magnesium injure the burn. BARTH (1) treated several kinds of paper with numerous salts and found that tri-potassium phosphate is injurious to the burn. GARNER (4) found di-potassium phosphate neutral in its effects upon the burn.

A consideration of the reason for the favorable action of the potassium salts of organic acids has led to several theories. SCHLOSING (15) attributes their favorable action to the fact that when heated they swell and yield a porous mass. NESSLER (12) says that the potassium salts are reduced and that potassium acts as an oxygen carrier; while GARNER (4) attributes their action to the fact that the salts are readily decomposed to yield carbonates. GARNER suggests that the carbonates may act favorably by alternately giving off and taking up carbon dioxide, or that small amounts of free potassium may be formed which may act as an

oxygen carrier. MAYER (10) also attributes the beneficial effects of the alkali salts to the fact that they are easily reduced. BARTH (1) suggests that the salts may have a beneficial action by raising the temperature of the leaf; he also attributes the harmful effect of the chlorides to the fact that they fuse and coat over the material, thereby preventing complete combustion.

Object

The object of this work is to study the effects of various salts closely related to the salts of potassium with a view to obtaining some light upon the conflicting theories. It has been suggested that the effect of the various salts upon the colloidal state of the material of the leaf may bear some relation to the problem. It was thought that probably potassium possesses some peculiar chemical properties which may account for its action.

Effect of salts upon combustion of tobacco

METHOD

The method of experimentation consisted of treating leaves and filter paper with various salts and noting their effect upon the fire-holding capacity. The samples of tobacco used in this work were of a single strain of a cigar filler type of tobacco grown in Pennsylvania under definite fertilizer treatments. The leaves previously had been well sweated. In all cases the solutions of the salts applied were 28.9 per cent normal. In order to see whether the effect of the salts was upon the colloidal state of the materials of the leaf, some of the leaves were rendered acid by treatment with 0.5 normal acetic acid, and others were rendered alkaline by a treatment with 0.2 normal solution of sodium hydroxide. The salts were applied by means of an atomizer, and then the leaves were placed under a bell jar to allow the salts to diffuse throughout the leaf. Knowing that different portions of the same leaf have different fire-holding capacities, in each test a portion of the tip, middle, and base of the leaf were used, and similar portions were saved for a check upon each leaf. The strip of leaf was ignited by means of a fishtail burner and the time of holding fire was determined by means of a stop watch. As would be

expected, due to variations in different leaves, the results were not always consistent in some cases where the comparative differences were small, but in each case a number of tests were carried out upon a number of different leaves until the average results were considered reliable for the purpose of comparing the effects of the various salts.

DATA

Because of the similarity in chemical behavior of the alkalies caesium, rubidium, potassium, sodium, and lithium, it was thought that a comparison of the effects of their salts upon the fire-

TABLE I

LEAVES FROM PLATS FERTILIZED WITH MANURE ONLY

Salt treatment	Other treatment	Number of tests	Average number of seconds holds fire	Average number of seconds increases fire-holding capacity
Rb_2CO_3	0.2/N NaOH	50	71	60
K_2CO_3	"	60	40	24
Na_2CO_3	"	60	18	5
Li_2CO_3	"	50	19	4
Rb_2CO_3	0.5/N acetic acid	10	59	45
K_2CO_3	"	60	44	35
Na_2CO_3	"	60	18	10
Li_2CO_3	"	50	19	13
Rb_2CO_3	Nothing	90	101	88
K_2CO_3	"	90	68	43
Na_2CO_3	"	60	34	11
Li_2CO_3	"	20	20	12

holding capacity of tobacco might throw some light upon the problem under consideration. The data obtained are indicated in the accompanying tables. The rubidium carbonate and caesium carbonate used were tested spectroscopically.

Tables I and II show that caesium, rubidium, and potassium carbonates greatly promote the fire-holding capacity of tobacco. Rubidium carbonate is always more effective than potassium, and in the case where the three salts were compared upon the same kind of leaves caesium carbonate was more effective than rubidium. The relative behavior of sodium and lithium suggests the possibility that their effect upon the precipitation of colloids may enter in as

a minor factor. According to HÖBER (5), the relative effectiveness of the alkalies in precipitating colloids in an acid medium is as follows: lithium > sodium > potassium > rubidium > caesium. In an alkaline medium the order is as follows: caesium > rubidium > potassium > sodium > lithium. In the cases where lithium is more

TABLE II

LEAVES FROM PLATS FERTILIZED WITH POTASSIUM CHLORIDE

Salt treatment	Other treatment	Number of tests	Average number of seconds holds fire	Average number of seconds increases fire-holding capacity
K_2CO_3	0.2/N NaOH	60	54	49
Na_2CO_3	"	60	21	14
Li_2CO_3	"	60	16	10
K_2CO_3	0.5/N acetic acid	20	27	24
Na_2CO_3	"	20	8	5
Li_2CO_3	"	20	9	6
Cs_2CO_3	Nothing	20	61	57
K_2CO_3	"	30	40	36
Rb_2CO_3	"	20	48	44

TABLE III

LEAVES FROM PLATS FERTILIZED WITH MANURE ALONE

Salt treatment	Other treatment	Number of tests	Average number of seconds holds fire	Average number of seconds increases fire-holding capacity
Potassium oxalate	0.2/N NaOH	70	42	19
Sodium oxalate	"	70	19	−3
Lithium oxalate	"	70	14	−6
Potassium oxalate	0.5/N acetic acid	100	33	21
Sodium oxalate	"	100	11	0
Lithium oxalate	"	100	14	2
Potassium oxalate	Nothing	50	37	21
Sodium oxalate	"	50	16	1
Lithium oxalate	"	50	13	−2

effective than sodium in the precipitation of colloids, it is also more effective in promoting the fire-holding capacity, and vice versa. Potassium, rubidium, and caesium, however, do not show this relation. This casts some doubt upon this principle of the behavior of sodium and lithium. At any rate, this effect upon the colloidal state of the materials of the leaf could be of only

minor importance. It seems very evident that of all the alkali carbonates only those of caesium, rubidium, and potassium materially aid the fire-holding capacity.

Table III shows that of the oxalates of potassium, lithium, and sodium, only the oxalate of potassium is effective in increasing

TABLE IV

LEAVES FROM PLATS FERTILIZED WITH MANURE ALONE

Salt treatment	Other treatment	Number of tests	Average number of seconds holds fire	Average number of seconds increases fire-holding capacity
Potassium citrate....	0.2/N NaOH	30	29	13
Sodium citrate.....	"	20	15	4
Lithium citrate.....	"	20	16	6
Potassium citrate....	0.5/N acetic acid	20	39	19
Sodium citrate.....	"	20	18	1
Lithium citrate.....	"	20	19	1
Potassium citrate....	Nothing	20	24	18
Sodium citrate.....	"	20	10	4
Lithium citrate.....	"	20	11	5

TABLE V

LEAVES FROM PLATS FERTILIZED WITH POTASSIUM CHLORIDE

Salt treatment	Other treatment	Number of tests	Average number of seconds holds fire	Average number of seconds increases fire-holding capacity
Potassium citrate....	0.2/N NaOH	50	28	18
Sodium citrate.....	"	50	11	2
Lithium citrate.....	"	50	10	0
Potassium citrate....	0.5/N acetic acid	20	37	30
Sodium citrate.....	"	20	10	3
Lithium citrate.....	"	20	5	−2

the fire-holding capacity. Here again in the cases where lithium is more effective than sodium in the precipitation of colloids, it is slightly more effective in promoting the fire-holding capacity.

From tables IV and V we see that potassium citrate is the only one of the 3 citrates which materially aids the burn. No correlation can be seen here between the effects of the salts upon the precipitation of colloids and their effect in increasing the fire-holding capacity.

Table VI shows a comparison of the results of a number of potassium salts. All of the potassium salts are very effective in promoting the fire-holding capacity, with the exception of the chloride, acid sulphate, and mono-potassium phosphate, which

TABLE VI

LEAVES FROM PLATS FERTILIZED WITH MANURE ALONE

Salt treatment	Number of tests	Average number of seconds holds fire	Average number of seconds increases fire-holding capacity
K_2CO_3	90	68	43
KCl	50	9	− 7
$KHSO_4$	40	7	−14
K_3PO_4	40	37	14
KH_2PO_4	40	16	−13
K_2HPO_4	40	42	13
K_2SO_4	30	53	29
Potassium oxalate	50	37	21
Potassium citrate	20	24	18
Potassium tartrate	50	64	48
Potassium acetate	50	45	29

TABLE VII

LEAVES FROM PLATS FERTILIZED WITH MANURE ALONE; LEAVES TREATED WITH 0.2/N NaOH, AND THEN WITH SALTS

Salt treatment	Number of tests	Average number of seconds holds fire	Average number of seconds increases fire-holding capacity
Na_2CO_3	60	18	5
NaCl	50	5	−1
$NaNO_3$	30	11	2
Na_2SO_4	20	6	1
Na_3PO_4	40	25	3
Na_2HPO_4	40	27	3
Sodium oxalate	70	19	−3
Sodium citrate	20	15	4
Sodium acetate	30	16	−5
Sodium tartrate	40	18	−5

are very injurious. Potassium carbonate and those salts which yield potassium carbonate when burned, tri-potassium phosphate, di-potassium phosphate, and potassium sulphate, improve the fire-holding capacity.

Table VII shows that sodium carbonate is the most effective of all of the sodium salts in promoting the burn. The other salts

are either nearly neutral or exert a harmful effect. It is quite evident that none of the sodium salts exert the marked beneficial effects which some of the potassium salts exert.

Effect of salts upon combustion of lump sugar

The effect of various salts of the alkalies upon the combustion of different kinds of paper and lump sugar was also studied; although, as one would expect, due to the dissimilarity of materials, the results in these cases were not always parallel with those upon tobacco. The results with lump sugar are particularly interesting. In each case a small portion of the salt was placed upon the lump of sugar and then an attempt was made to burn the sugar by touching it to a gas flame. The results obtained are indicated in table VIII.

Discussion

SCHLOSING (15) attributed the favorable action of the organic salts of potassium to the fact that they swell up and yield a porous mass. NESSLER (12) combated this idea and showed that other salts of potassium which do not swell so much when heated also have a favorable action in promoting the fire-holding capacity of tobacco. GARNER showed that the carbonates of potassium are just as effective as the organic salts. From tables VI and VII we see that both potassium sulphate and tri-potassium phosphate, as well as potassium carbonate, promote the fire-holding capacity. These results confirm the conclusions of NESSLER and GARNER, and indicate that the good effects of the potassium salts of organic acids cannot be attributed to the fact that they swell and yield a porous mass when heated.

NESSLER (12) suggests that potassium salts are reduced and that small amounts of elemental potassium may act as an oxygen carrier. It is true that the salts of potassium which have a favorable action upon the fire-holding capacity are all salts of acids which are in a highly oxidized condition. Although no direct data could be found which would show the relative ease of reduction of the alkali carbonates, there are data upon the electrolytic solution tension of the alkalies. The order of the alkalies according to their decreasing electrolytic solution tension is as follows: caesium, rubidium, potassium, sodium, and lithium. The same order

represents their increasing ease of reduction in solution. If we assume that this represents the order of the ease of reduction of the

TABLE VIII

EFFECT OF SALTS UPON THE COMBUSTION OF LUMP SUGAR

Salt	Effect
K_2C_3O	Lump of sugar burned with flame; sugar coaled
Rb_2CO_3	" " " " " " " "
Cs_2CO_3	" " " " " " " "
Na_2CO_3	" " " " " " " "
Li_2CO_3	" " " " " " " "
K_2SO_4	Lump of sugar burned slightly; sugar coaled slightly
K_2HPO_4	Lump of sugar burned; sugar coaled
KH_2PO_4	Lump of sugar burned slightly; sugar coaled slightly
K_3PO_4	Lump of sugar burned with flame; sugar coaled
KCl	" " " " " " " "
KNO_3	Lump of sugar burned with flame, sputtered; sugar coaled
Potassium acetate	Lump of sugar burned with flame; sugar coaled
Potassium citrate	" " " " " " " "
Potassium oxalate	" " " " " " " "
Potassium tartrate	" " " " " " " "
LiCl	" " " " " " " "
Lithium oxalate	" " " " " " " "
Lithium citrate	" " " " " " " "
NaCl	Lump of sugar burned slightly; sugar coaled
Sodium tartrate	Lump of sugar burned with flame; sugar coaled
Sodium oxalate	" " " " " " " "
Without salt	Lump of sugar melted, would not burn; did not coal
$LiSO_4$	Sugar melted; did not burn with flame; did not coal
Na_2SO_4	Lump of sugar burned slightly; sugar coaled slightly
$CaCO_3$	Sugar melted; did not burn with flame; did not coal
Pb_3O_4	Lump of sugar burned with flame; sugar coaled
$BaCO_3$	" " " " " " " "
$KMnO_4$	" " " " " " " "
Fine metallic iron	Lump of sugar burned with difficulty
Platinized asbestos	" " " " " "
Zinc filings	" " " " " "
Copper filings	" " " " " "
Finely powdered glass tubing	Lump of sugar burned with flame; sugar coaled
Finely powdered charcoal	Lump of sugar burned with flame
Carbonized sugar	" " " " " "

alkali carbonates, it would be difficult to explain by NESSLER's theory why lithium and sodium carbonates are not effective, and caesium, rubidium, and potassium carbonates are effective.

GARNER (4) suggests that the carbonate might act favorably by alternately giving up and taking on carbon dioxide. We have seen that caesium, rubidium, and potassium carbonates are very much more effective than the carbonates of sodium and lithium. At 700° C. the order of the alkali carbonates according to their increasing ease of dissociation is as follows: potassium, rubidium, sodium, caesium, and lithium. Lithium carbonate is dissociated into carbon dioxide and lithium oxide to a much greater degree at 700° C. than any of the other carbonates (9). If potassium carbonate acts favorably by alternately giving off and taking up carbon dioxide, it is difficult to see why lithium carbonate should not be even more effective. It seems, therefore, that this theory will not explain the beneficial action of the caesium, potassium, and rubidium carbonates.

From table VIII we see that all of the salts which were effective in increasing the fire-holding capacity of tobacco will cause the lump of sugar to burn with a flame when ignited by means of a gas burner. Some of the salts which were only slightly effective in increasing the fire-holding capacity of tobacco, such as lithium carbonate and sodium carbonate, are effective also in promoting the combustion of sugar with the production of a flame. Here again caesium, potassium, and rubidium carbonates are particularly active. BARTH (1) has suggested that the salts present in the leaf may aid in the combustion by raising the temperature of the leaf, the effect being somewhat analogous to the effect of salts upon raising the boiling point of water. As shown in table VIII, such substances as metallic filings, powdered glass, and carbonized sugar when used in larger quantities also are effective in causing the lump of sugar to burn. From these results obtained upon lump sugar, it would seem as though their effect in raising the temperature might be of significance. But with this theory alone it would be difficult to account for the differences in degree of action of the various salts. Also it would be difficult to explain why some of the salts have no effect, while others have a very

marked effect in promoting the combustion of tobacco. SLIGH and KRAYBILL (16) have determined the temperatures of burning cigars and have found some evidence which suggests that the moisture content as well as the composition of the cigar has an effect upon the burning temperature. It is planned to study this problem further with the object of determining the extent to which this hypothesis may be applied.

BARTH (1) considers the harmful effect of chlorides to be due to the fact that they fuse and coat over the material, thereby preventing complete combustion. SLIGH and KRAYBILL (16) found the temperature in the cigar varying from 813° C. to 925° C. during a puff, and from 584° C. to 803° C. at stationary temperatures between the puffs. It is doubtful whether the temperature of the burning strip of a leaf of tobacco would be as high as these stationary temperatures of the cigar. The temperature of the leaf then would not be high enough to fuse pure sodium chloride or pure potassium chloride. It would seem then as though the theory of BARTH would not account for the harmful effect of the chlorides. An objection might be raised from the standpoint that we have in the leaf mixtures of salts, and that their fusing points would be lower than that of the pure salts. The fusing point of sodium chloride is about 820° C., and that of rubidium carbonate is 837° C. (9). It would be difficult to understand why one salt should harm the burn by fusing and the other should not harm the burn when they fuse at almost the same temperature.

An attempt was made to tabulate and compare the chemical and physical properties of these salts with the hope of finding some explanation of their action. Among the properties compared were the melting points, specific heats, speed of vaporization, and dissociation pressure of the carbonates. A very careful comparison of the chemical and physical properties of the salts does not seem to offer any explanation of their action. It is true that the order of effectiveness of the caesium, rubidium, and potassium carbonates is the same as their increasing electrolytic solution tension, and also the same as their increasing atomic weights. The question might be raised as to whether their behavior might

not be due in part to the alkalinity of the salts in solution. Such an explanation, however, would not account for the behavior of the sodium and lithium carbonates.

Extremely small amounts of caesium, potassium, or rubidium carbonates greatly increase the fire-holding capacity of the tobacco. A 2 per cent solution of potassium carbonate applied by means of an atomizer to the leaf was sufficient to produce the effect. Upon examining the ash left after the combustion, the potassium was found as the carbonate, that is, in the same form in which it was present before the combustion. It is possible, therefore, that certain salts, such as the carbonate, phosphate, and sulphate of potassium, and the carbonates of rubidium and caesium, act in a catalytic manner to promote the combustion of the tobacco leaf. In the combustion of lump sugar other salts are also effective, but the carbonates of caesium, potassium, and rubidium are more effective. Here the effect of the salts in raising the temperature may be important.

According to this assumption, caesium carbonate, potassium carbonate, rubidium carbonate, tri-potassium phosphate, di-potassium phosphate, and potassium sulphate have a catalytic action favoring the combustion of the tobacco leaf. The salts of sodium and lithium, potassium chloride, mono-potassium phosphate, and acid potassium sulphate do not have this catalytic action. The harmful effects of the chlorides seem to be due to a negative catalytic action.

It is possible that a careful study of the chemical action resulting when various organic materials, such as filter paper, and sugar treated with the salts, are subjected to temperatures close to the temperature of the burning cigar may help to explain the action. Nef (11) has studied the effect of alkalies upon the oxidation of sugars in solution at low temperatures. It may be that a study of the rate of oxidation of various organic salts of the alkalies when subjected to high temperature may furnish a better explanation of the effect of the potassium salts. Studies along these lines are planned. It may be that more than one factor plays a rôle in determining the action of the various salts, resulting in a complex situation.

Summary

1. The alkali carbonates of caesium, rubidium, and potassium have a definite marked effect in promoting the fire-holding capacity of tobacco, which sodium and lithium carbonates do not exhibit, the order of effectiveness being as follows: caesium, rubidium, potassium.

2. Of the oxalates tried, only potassium is effective. In the case of the carbonates and the oxalates in an alkaline medium, where lithium is more effective than sodium in the precipitation of colloids, it is slightly more effective also in promoting the fire-holding capacity. In the case of the citrates there is no such relation and, in the case of the carbonates, potassium, rubidium, and caesium do not behave in this manner. It is doubtful, therefore, whether the effect of the salts upon the colloidal state of the tobacco leaf is of any significance.

3. Only potassium citrate is effective in promoting the burn. The citrates of sodium and lithium are nearly neutral in their effect.

4. The organic salts of potassium, potassium carbonate, tri-potassium phosphate, di-potassium phosphate, and potassium sulphate improve the fire-holding capacity; while potassium chloride, acid potassium sulphate, and mono-potassium phosphate are injurious to the burn.

5. Sodium carbonate improves the fire-holding capacity slightly, while all of the other sodium salts are either neutral or injurious to the burn.

6. The data obtained do not confirm the idea that the reduction of the potassium salts will account for their favorable action.

7. Data are given which indicate that the harmful action of chlorides is not due to the fact that they fuse, as was suggested by BARTH.

8. Data are given which indicate that the alternately giving off and taking up of carbon dioxide will not account for the beneficial effects of potassium carbonate.

9. The effect of the salts in raising the temperature of the leaf may be of some significance.

10. The problem is probably complex, and the action of the caesium, potassium, and rubidium salts may be due to a number of complex factors.

11. It seems probable that caesium, potassium, and rubidium in the form of certain salts, such as the carbonates, sulphates, and phosphates, have a specific catalytic action in the combustion, and that the chlorides have a negative catalytic action. It is planned to study the rate of decomposition of various organic salts of the alkalies, and also the decomposition products of various organic substances treated with salts of the alkalies, when subjected to temperatures which are attained in the burning cigar.

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NOTES ON NEW OR RARE SPECIES OF RAVENELIA

W. H. Long

While on recent field work in Texas, the writer collected several very interesting species of *Ravenelia*. Some of them are undescribed, while others have heretofore been known only from their type collections. Several of them are Mexican, while one is a South American species.

Ravenelia hoffmanseggiae, sp. nov.

O. Pycnia unknown.

II. Uredinia amphigenous, scattered, orbicular to irregularly oval, liver brown,[1] subepidermal, ruptured epidermis prominent; paraphyses none; urediniospores obovate, ellipsoid to subglobose, 16–25 by 25–30 μ, average for 10 spores 19.7 by 26.7 μ, walls thin, 1–1.5 μ, uniform in thickness and concolorous, capucine buff in color, sparsely and minutely echinulate when dry but appearing as if smooth when wet; germ pores 8, situated in two irregular rows of 4 each, one row subequatorial, the other near apex of spore, in the subglobose spores the germ pores appear as if scattered.

III. Telia unknown.

On Cassiaceae. Type collected on *Hoffmanseggia oxycarpa* at Del Rio, Texas, November 6, 1916, by *W. H. Long* (no. 6082).[2] This is the first collection of *Ravenelia* to be reported on this host, although the genus *Hoffmanseggia* is widely distributed throughout those regions where species of *Ravenelia* flourish.

Ravenelia siderocarpi, sp. nov.

O. Pycnia unknown.

II. Uredinia amphigenous but mainly epiphyllous, scattered, bullate to oval, 0.1–0.8 mm. across, often in a circle around a central sorus, chestnut-brown, subcuticular, long covered by the cuticle, ruptured cuticle very prominent; paraphyses none;

[1] Ridgway, Robert, Color standards and color nomenclature. pp. 43. *pls.* 53. Washington, D.C. 1912.

[2] Unless otherwise stated, all herbarium numbers cited in this article refer to the herbarium numbers of the writer.

urediniospores obovate, obovate-elliptical to subpyriform, 15–18 by 25–37 μ, average for 20 spores 16.9 by 31.7 μ, walls ochraceous-tawny, concolorous, thick, 2.5–3.5 μ, apex but slightly if at all thickened, echinulate; germ pores prominent, 6 in equator.

III. Telia amphigenous, usually epiphyllous, sparse, scattered, small, 0.1–0.5 mm. across, bullate to elliptical, subcuticular, blackish-brown, tardily naked, ruptured cuticle very conspicuous; paraphyses none; teliospore heads chestnut-brown, subglobose, 40–60 μ in diameter, average for 20 heads 50.5 μ, 2–4 spores across, 5–10 spores to each head, 4–8 marginal, 0–3 inner spores, usual number of spores per head 7–8, each spore bearing 3–6 short hyaline tubercles 3–5 μ long; cysts few, 4–8, as many as the marginal spores, subglobose, subpendant around pedicel, not cohering, easily swelling and bursting in water; pedicel hyaline, short, deciduous, compound.

On Mimosaceae. Type collected on *Siderocarpos flexicaulis* 6 miles from Brownsville, near Tandy's Switch, Texas, November 11, 1916, by *W. H. Long* (no. 6174). This *Ravenelia* is very abundant on this host in the Texas ebony jungles in the immediate vicinity of Brownsville. It is probably common wherever its host is found in sufficient quantity to form thickets.

Ravenelia prosopidis, sp. nov.

O. Pycnia unknown.

II. Uredinia sparse in material examined, small, amphigenous, mainly epiphyllous, often in a circle around a central sorus, 0.5–1.0 mm. across, narrowly elliptical to oval, subepidermal, long covered by the epidermis, ruptured epidermis very prominent; urediniospores oval to subpyriform, 13–20 by 24–41 μ, strontium yellow, average for 40 spores, 16.9 by 31.6 μ; walls 1.5–2 μ thick, apex slightly darker and thicker, verrucose-echinulate, germ pores 4–6 in equator; paraphyses abundant, of two types, the usual form capitate, the other broadly clavate, in a dense ring around the sorus, also intermixed with the spores, heads of capitate paraphyses madder brown, walls thickened at apex, stipe amber yellow to hyaline, solid, 12–27 by 28–85 μ, average for 40, 16.84 by 55.5 μ, clavate paraphyses 10–13 by 25–45 μ, average for 10, 13.6 by 39 μ.

III. Telia amphigenous, mainly hypophyllous, Vandyke brown, usually in a circle around a central sorus, 0.5–1.0 mm. across,

elliptical to oval, subepidermal, early naked, ruptured epidermis very prominent; teliospore-heads tawny, depressed hemispherical, often concave at top, 75–118 μ, average for 40 heads 94 μ, 6–10 spores across, 20–28 marginal spores, 16–40 inner spores, usual number for head 46–54 spores in all; heads papillate, with one, rarely two, papillae to each spore, papillae ranging from mere tubercles near top of head to blunt papillae 4–7 μ long around margin, top of heads often free from papillae, many heads with only a few tubercles on entire head, papillae light brown; paraphyses very abundant in a dense circle around the telia, also scattered throughout the sorus, similar to those found in the uredinia, often sori occur which are composed mainly of paraphyses; cysts numerous, pendant in 2 or 3 rows around the pedicel, subglobose, about as many as marginal spores, easily swelling and bursting in water; pedicel compound, deciduous, hyaline to faintly fulvous, short.

On Mimosaceae. Type collected on *Prosopis juliflora* at Denton, Texas, October 10, 1907, by *W. H. Long* (no. 2013); also collected on same host and in same locality in 1908 by *Long* (no. 4870). A part of the type material of this *Ravenelia* was issued in *Fungi Columbiani*, E. BARTHOLOMEW, no. 2681, as *Ravenelia arizonica* Ellis and Ev.

Ravenelia prosopidis is closely related to *R. arizonica*, but differs from this species in the very irregular length of its papillae and in having some teliospore heads nearly smooth. Its telia are also encircled by a dense layer of paraphyses, while none or but very few paraphyses are found in the telia of *R. arizonica*. This species will probably be found throughout northern Texas within the range of its host. It is sometimes associated on the same leaves with *Neoravenelia holwayi*, at least some telia were found which contained teliospores with heads entirely smooth, while other and adjacent sori contained the typical papillate heads of *R. prosopidis*.

RAVENELIA ROEMERIANAE Long

O. Pycnia sparingly present, amphigenous and fruticolous, in orbicular groups of 6–20, groups 0.5–1.0 mm. across, usually surrounded by a circle of uredinia, blackish-brown, flattened hemispherical, 70–105 μ across, 25–38 μ tall.

II. Uredinia usually fruticolous but also amphigenous, occasionally caulicolous and in very rare cases forming slight witches'

brooms, often densely confluent on both sides of the pods over areas 1–5 cm. across; individual uredinia on pods elliptical to irregularly oval, 0.2–0.6 mm. across, verona brown to tawny-olive in color, uredinia on leaves amphigenous, elliptical to irregularly oval, primary uredinia often encircling pycnia; urediniospores obovate-oblong to linear-oblong, on pods 10–17 by 27–45 μ, average for 20 spores 13 by 31 μ, on leaves urediniospores are 10–14 by 27–38, average for 20 spores 13 by 33 μ, average for both sets of spores 13 by 32 μ; walls 1–1.5 μ thick, slightly thicker above (about 3 μ), prominently but sparsely echinulate, spinules very sparse on upper third of spore, upper third golden brown to wine color, remainder of spore paler to hyaline, germ pores 8, in 2 rows of 4 each, upper row at boundary of colored and hyaline part of spore, lower row about the same distance below the equator; paraphyses abundant, intermixed with the urediniospores, clavate to clavate-capitate, 35–50 μ long, average length for 10, 44.0 μ, heads 9–13 μ, average for 10 heads 10 μ, apex of head thickened about 3 μ, pale fulvous, stipe usually thin-walled, hyaline.

III. Telia amphigenous, often abundant on all parts of badly infected leaves, scattered, subcuticular, blackish, shining, 0.2–1.2 mm. across, irregularly oval, ruptured cuticle noticeable; teliospore heads blackish, 63–100 μ, average for 30 heads 78 μ, 5–7 cells across, 14–30 spores in each head, 8–14 marginal spores and 6–15 inner ones, verrucose, each spore bearing 3–10 colorless warts about 2 μ tall by 3 μ broad; paraphyses present and similar to those in uredinia; cysts of same number as marginal spores, flattened, appressed beneath head, extending from periphery to pedicel, in one row, united laterally, ovoid to oblong-ovate, slow to burst in water; pedicel short, colorless, compound, deciduous.

DISTRIBUTION.—TEXAS: On *Acacia roemeriana*, San Marcos (type locality), *Long*, in November 1915 (nos. 5494 and 5498 type), in May 1916 (nos. 6009, 6019, 6020, and 6065); San Antonio, *Long*, in May 1916 (nos. 5610, 5611, 5612, 5614, and 5615), and in November 1916 (nos. 6155 and 6159); Uvalde, *Heald* and *Wolf*, in August 1909 (no. 6243); *Long*, in November 1916 (nos. 6145 and 6148).

The type of *Ravenelia roemerianae* was collected on *Acacia roemeriana* at San Marcos, Texas, in November 1915, but on account of the lateness of the season this material did not contain any uredinia. In May 1916, the writer

visited the type locality of this rust at San Marcos and found an abundance of uredinia, especially on the pods. Some uredinia as well as pycnia were also found on the leaves. Even at that early date telia were developing and the uredinia on the leaves were disappearing. The uredinia which were so abundant on the pods in May weathered and disappeared so that none were found on the pods in November of the same year.

The writer has seen several thousand trees of *Acacia roemeriana* infected with this *Ravenelia* in various places in Texas, and only two trees of this entire number showed any evidence of witches' brooms. One tree was found at San Antonio and the other at Uvalde, Texas. There were some 10–15 witches' brooms on each of these two trees. Apparently the germination of the teliospores of this rust occurs when the pods are young and easily infected and yet not at the right season to infect the young branches and cause witches' brooms.

This rust is closely related to *Ravenelia versatilis* (Peck) Dietel, a fact noted in a previous article[3] by the writer. Table I gives a brief comparison of the more salient characters of each of these two species of *Ravenelia*. From this table the main differences between the two species are easily seen.

Ravenelia roemerianae has been collected by the writer in several places in Texas and probably occurs wherever the host is present. The rust was exceedingly abundant in the vicinity of Uvalde, Texas, in November 1916. Every tree of *Acacia roemeriana* examined by the writer in the mesquite (*Prosopis juliflora*)-catclaw (*Acacia roemeriana*) flats was heavily infected; in fact every leaf on most of the trees was practically covered with the blackish telia of this rust.

RAVENELIA MESILLANA Ellis and Barth. Bull. Torr. Bot. Club **25**:508. 1898

(*Ravenelia longiana* Sydow, Hedwigia Beibl. **40**:128. 1901)

O. Pycnia, appearing before the uredinia, sparse, amphigenous, in circinating, crowded, orbicular groups 2–4 mm. across, subcuticular, Brussels brown, depressed hemispherical, 40–60 μ tall by 100–165 μ broad.

II. Uredinia amphigenous, mainly hypophyllous, scattered, tawny, oval to elliptical, 0.5–1.0 mm. in diameter, early naked, pulverulent, subcuticular, ruptured cuticle very noticeable; urediniospores oval to subglobose, 15–22 by 20–26 μ, average for 20 spores 19 by 23 μ; walls 2–3 μ thick, tawny-olive, sparsely echinulate, germ pores 6–8, scattered; paraphyses very few, intermixed with

[3] LONG, W. H., Five undescribed species of *Ravenelia*. BOT. GAZ. **61**:416–424. 1916.

TABLE I

Species	Uredinia	Urediniospores	Paraphyses	Telia heads	Cysts
Ravenelia roemerianae	Usually on pods	10–17×27–45 μ, average for 40 spores 13×32 μ	6–13×32–54 μ, average 11×43 μ	63–100 μ, average 78 μ, marginal spores 8–14, inner spores 6–15, usual number per head 20–26, 5–7 across, heads verrucose	Flattened, appressed, in 1 row
Ravenelia versatilis . . .	Usually on leaves and young twigs, forms witches' brooms	9–16×16–27 μ, average for 40 spores 12×23 μ	8–16×27–57 μ, average 12×38 μ	53–90 μ, average 71.6 μ, marginal spores 5–18, inner spores 3–20, usual number per head 34–36, 5–7 cells across, heads smooth	Flattened, appressed, in 1 row

the spores, colorless, clavate to subcapitate, 5–14 by 35–62 μ, average for 20, 9.6 by 45 μ, apex of head thin-walled, base of head very thick-walled, stipe usually solid.

III. Telia amphigenous, scattered, 0.5–1.0 mm. across, often confluent over areas 3–4 mm. in diameter, brownish-black, elliptical to irregularly oval, subcuticular, ruptured cuticle very conspicuous; teliospore heads dark chestnut-brown, hemispherical, smooth or an occasional head with a few scattered, short (2–3 μ), hyaline, tubercles, especially on the marginal spores, 5–9 cells across, 60–90 μ, average for 20 heads 74 μ, 10–20 marginal spores, 8–24 inner spores, usual number per head 24–32; paraphyses present but very few and similar in every way to those found in the uredinia; cysts hyaline, in 2–3 rows around the pedicel, many, not coherent with each other, slow to burst in water, subpendant; pedicel colorless, compound, short, deciduous.

This description of the rust was drawn from material on *Cassia roemeriana*.

DISTRIBUTION.—NEW MEXICO: On *Cassia bauhinioides*, Mesilla Park, *Wooton*, in October 1895, ex. Herb. N.Y. Bot. Garden (no. 5021 *Long*) and ex. Herb. A. and M. College of N. Mex. (no. 5022 *Long*); *Wooton* in October 1897, *North American Fungi*, Herb. of ELAM BARTHOLOMEW (part of type material. no. 5025 *Long*); mesa west of Organ Mountains, *F. C. Werkenthin*, in October 1916 (no. 5480 *Long*); TEXAS: On *Cassia roemeriana*, Austin, November 1897 (no. 5039), type material for *Ravenelia longiana*, *Long*, in August 1901 and October 1915 (nos. 1019 and 5481); Llano, *Heald* and *Wolf*, August 1909 (no. 1751 Herb. Path. and Myc. Investigat., Plant Disease Survey); Marble Falls. *Carsner* and *Studhalter*. May 1912 (no. 4333 Herb. Univ. Texas); Meridian, *Long*. June 1916 (no. 6056); San Antonio, *Long*, May and November 1916 (nos. 5616 and 6168); San Marcos, *Long*, November 1915, and May 1916 (nos. 5468 and 6034).

This *Ravenelia* was first collected on *Cassia bauhinioides* at Mesilla Park, New Mexico, in 1895 and again in 1897 by WOOTON. It was described as a new species by ELLIS and BARTHOLOMEW from the New Mexico material collected in 1897. It has been reported on this host only from the type locality. In 1900, the writer sent SYDOW a *Ravenelia* on *Cassia roemeriana*, collected at Austin, Texas. in 1897. From this material he described as new, *Ravenelia longiana*.

In recent investigations on the genus *Ravenelia*, the writer's attention was called. not only to the marked resemblance of *R. mesillana* to *R. longiana*, but also to the close relationship of the two host plants, *Cassia bauhinioides* and *C. roemeriana*. The only appreciable difference heretofore reported between the two rusts was the supposed fact that *Ravenelia mesillana* had no paraphyses,

while *R. longiana* had a few hyaline ones. The writer has material from the type collections of both of these species, and a careful examination of this material shows that not only do both species have paraphyses, but that the paraphyses are identical in every respect and are present in the telia of the type material of both *R. mesillana* and *R. longiana*. A careful study of the other salient characters of these rusts has convinced the writer that they are identical in every respect and therefore should be considered as only one species.

In recent field work in Texas, the writer collected the pycnidial stage on *Cassia roemeriana* of what has heretofore been known as *Ravenelia longiana*.

Ravenelia siliquae Long

O. Pycnia unknown.

II. Uredinia hypophyllous and caulicolous, on the leaves scattered, elliptical, 0.5–1.0 mm. across, pulverulent, subcuticular, early naked, sudan brown, ruptured cuticle not prominent, uredinia on the woody twigs and branches perennial, very inconspicuous, elliptical, 0.5–5 mm. long by 0.5–2 mm. broad; urediniospores obovate, elliptical to rarely oblong, on the leaves 13–17 by 20–27 μ, average for 10 spores 14.4 by 21 μ, urediniospores on branches 11–16 by 17–27 μ, average for 20 spores 13.4 by 22.5 μ, urediniospores on both leaves and branches buff yellow; walls 1.5–2.5 μ thick, concolorous, not thickened at apex, densely and strongly verrucose, germ pores 8, in two transverse zones of four each, equidistant from the equator; paraphyses abundant, intermixed with the spores, clavate to subcapitate, often curved, 7–10 by 50–67 μ, average for 10 paraphyses 9.5 by 62 μ, heads pale fulvous to hyaline, stipe slender, usually solid, hyaline, paraphyses in sori on woody branches few, 6–11 by 25–49 μ, average for 20 paraphyses 8.3 by 38 μ.

III. Telia unknown.

On Mimosaceae: Distributed as follows: Texas, on *Acacia farnesiana*, San Antonio, *Long*, November 1916 (no. 6153); *W. H. Mercer*, February 1917 (no. 6263); Mexico, on *Acacia farnesiana*, Etla, Oaxaca, *Holway*, October 1899, no. 3841 of *Holway* (type); Hawaii, on *Acacia farnesiana*, Honolulu, *Harold L. Lyon*, January 1913, no. 164, Sydow, *Fungi exotici exsiccati*.

The rust on the pods of this host from Hawaii agrees very closely with the Mexican type material. There are a few minor differences in the characters of this rust when on leaves and stems and when on the pods, but they are not sufficient in the judgment of the writer to constitute a new species. From the foregoing distribution it is seen that since this *Ravenelia* was described in 1903

on the pods of *Acacia farnesiana* from Mexico, the rust has been collected in Texas on the leaves and woody branches of this host and in Hawaii on the pods. It was probably introduced into Hawaii on nursery stock which contained infected woody branches. Apparently *Ravenelia siliquae* does not have a telial stage, since only uredinia have ever been found, although this rust has been collected during October, November, January, and February on pods, leaves, and woody branches, and in three countries, namely, United States, Mexico, and Hawaii.

Ravenelia australis Diet. and Neg.

O. Pycnia unknown.

II. Uredinia amphigenous, very small, punctiform to irregularly oval, less than 0.5 mm. across, subepidermal, soon naked, ruptured epidermis inconspicuous; urediniospores obovate, elliptic-obovate to subpyriform, light cinnamon brown, 13–20 by 25–32 μ, average for 20 spores 16.6 by 28.2 μ; walls 1.5–2.0 μ thick, slightly or not at all thickened above, concolorous, echinulate, germ pores 4–6, equatorial; paraphyses very abundant, incurved, dense, encircling the sori, ferruginous, hyphoid, more or less curved near apex, 10–17 by 50–67 μ, average for 10 paraphyses 12.5 by 14.4 μ, walls about 2.5 μ thick, an occasional paraphysis clavate, nearly colorless and with a solid stipe.

III. Telia amphigenous, punctiform to irregularly oval, less than 0.5 mm. across, blackish-brown, subepidermal, early naked, ruptured epidermis inconspicuous; paraphyses very abundant, encircling the sori and similar to those found in the uredinia; teliospore heads chestnut-brown, hemispherical, 67–110 μ across, average for 20 heads 92.3 μ, 7–11 cells across, 18–30 marginal spores, 22–64 inner ones, 40–94 spores per head, smooth; cysts small, numerous, subglobose, subappressed, beneath entire head, in two rows, swelling and easily bursting in water; pedicel short, hyaline, deciduous.

On Mimosaceae.—The following collections were made by the writer in Texas, all on *Acacia farnesiana:* Uvalde, November 1916 (nos. 6150, 6151, and 6152); San Antonio, November 1916 (no. 6165). The above is a description of rust as it occurs in Texas.

This species of *Ravenelia* has heretofore been known only from its type locality in South America (Concepcion, Chile), where it was found on *Acacia cavenia*, now recognized as a synonym for *A. farnesiana* (*Vachellia farnesiana*).

The writer has not been able to obtain authentic material of this South American *Ravenelia*, nevertheless he is assigning to this species the Texas *Ravenelia* collected on the same host (*A. farnesiana*), since its characters are practically identical with those described for the South American plant.

RAVENELIA GRACILIS Arth.

O. Pycnia not found in the Texas material.

II. Uredinia epiphyllous, seated on slightly pallid areas, scattered, very small, less than 0.4 mm. across, elliptical to irregularly oval, tardily naked, subepidermal, ruptured epidermis prominent; urediniospores ovate, ovate-fusiform to somewhat flask-shaped, usual shape ovate-flask-shaped, 15–21 by 30–45 μ, average for 20 spores 18.4 by 37.6 μ; walls 2–2.5 μ thick, russet colored, sparingly echinulate, apex darker and slightly thickened, germ pores 4–6, in equator; paraphyses few, peripheral and also intermixed with the spores, hyphoid to subclavate, hyaline, walls thin, 4–7 by 35–50 μ.

III. Telia epiphyllous, similar in size and shape to the uredinia, blackish-brown, subepidermal; teliospore heads dark chestnut-brown, hemispherical, 60–87 by 37–40 μ thick, average for 20 heads 73.8 by 39 μ, 5–6 spores across, 8–14 marginal spores, 4–12 inner spores, usual number per head 22–24, each spore on lower part of head bearing 2–4 small, hyaline tubercles, 2–5 μ long, upper portion smooth, or with 1–4 very short tubercles to each spore; cysts in 1 row, subglobose, few, as many as the marginal spores, united laterally and extending from periphery to stipe, subappressed, easily swelling and bursting in water; pedicel short, deciduous, colorless.

Collected on *Havardia brevifolia*[4] 6 miles from Brownsville, Texas, near Tandy's Switch, November 10, 1916, by *W. H. Long* (no. 6160). This description was made from material collected at Brownsville, Texas.

This rust has heretofore been known only from the type collection which was made at San Luis Potosi, Cardenos, Mexico, on an unknown host. The writer recently collected at Brownsville, Texas, what appears to be the same species. A careful comparison of the type material collected by HOLWAY in Mexico with the Brownsville rust shows no essential characters sufficient to warrant making a new species of the Texas *Ravenelia*. A study of the Mexican

[4] The writer is under obligations to Dr. J. K. SMALL, of the New York Botanical Garden, for identifying this host and the host of *Ravenelia hoffmanseggiae*.

host and of the host found at Brownsville shows that the two are apparently identical. *Ravenelia gracilis* was rather common in the vicinity of Brownsville wherever the host occurred in any quantity. In the original description of this species the urediniospores are given as obovate and the teliospore heads as bearing 4–7 colorless tubercles to each spore. The writer, however, failed to find any obovate urediniospores in that portion of the type collection which is in his herbarium. The teliospore heads of the type show many heads with smooth tops but with short tubercles around the margin, while other heads in the same mount have shorter and fewer warts to each spore at the top than on the margin, thus agreeing in every detail with the Brownsville material.

Ravenelia leucaenae Long

This species was collected by the writer near Brownsville, Texas, on *Leucaena pulverulenta*. There are certain minor characters of this rust not given in the published description of it that are worth recording. The urediniospores on this host are mainly concolorous, often with the apex slightly thickened. The teliospore heads are 5–6 cells across, with 5–16 marginal spores and 3–14 inner ones, usual size 14–16 spores per head, each spore at top of head bears from 0 to 2–4 very short tubercles, while there are 4–6 straight or slightly curved tubercles, 4–6 μ long, on each marginal spore; cysts as many as marginal spores, appressed, extending from periphery to pedicel.

This *Ravenelia* has been reported from Mexico on the following host species: *Leucaena* sp., *L. diversifolia*, and *L. esculenta*.

Neoravenelia holwayi (Dietel) Long

II. Uredinia caulicolous, forming large, woody, perennial, fusiform galls, 1–8 cm. thick by 4–12 cm. long, densely confluent over large areas on the galls, subepidermal, argus brown; urediniospores oblong-linear, obovate, elliptical, clavate to subpyriform, usual shape obovate to subclavate, 13–24 by 26–53 μ, average for 120 spores 17 by 36 μ; walls 2–3 μ thick, slightly thickened above, sudan brown, often lighter to subhyaline below the equator, echinulate, germ pores 4–6 in equator; paraphyses few, capitate or sometimes clavate-capitate, 13–22 by 30–65 μ, average for 10 paraphyses 17.6 by 46.3 μ, heads intensely colored, deep chestnut-brown to liver brown, nearly solid, stipe hyaline or faintly tinted.

III. Teliospores intermixed in uredinia on the galls; teliospore heads liver brown, hemispherical, often depressed, smooth, 60–130 μ, average for 40 heads 103 μ, 8–12 spores across, 20–38 marginal spores, 40–78 inner ones, average number of spores in each head 84–94; cysts globose to subglobose, in 2–3 rows, pendant beneath entire head, not coherent, slow to burst in water; pedicel hyaline or slightly tinted, short, deciduous, compound. This is a description of the gall-producing form of *Neoravenelia holwayi*.

For several years the writer has been finding a species of *Ravenelia* on mesquite (*Prosopis juliflora*) which produces large, fusiform, woody galls. At first this rust was referred to *Ravenelia arizonica*, but a careful examination of the galls revealed the presence of teliospores with smooth heads. These smooth teliospores were so constantly found associated with certain types of galls that the writer made a special study of the galls found on mesquite. This investigation showed that there was a *Ravenelia* present on galls throughout a certain zone which constantly produced smooth teliospore heads. A careful study of the *Ravenelia* on these galls failed to show any positive differences either in the urediniospores or teliospores which would separate this gall-forming species from the ordinary leaf form of *Neoravenelia holwayi*. There are wide variations in shape and size of the urediniospores, as is to be expected when growing on galls as compared to those found on the leaves.

The galls were found in localities where the leaves of the mesquite were abundantly infected with the usual form of *N. holwayi*. In the vicinity of San Antonio and Uvalde the galls were rare, but at Corpus Christi and Brownsville they were rather common. From Del Rio west to New Mexico and Arizona all of the galls found on the mesquite were of a different type and were associated with the teliospores of *Ravenelia arizonica*. The galls produced by *Neoravenelia holwayi* are smoother and more fusiform than those caused by *Ravenelia arizonica*. In *R. arizonica* the galls are rather brittle, due to the large amount of parenchyma tissue developed in the gall. On weathering, even when alive these galls have deep transverse fissures in their surfaces. The galls produced by *Neoravenelia holwayi* are very woody, rather smooth, do not develop many fissures, but form round wartlike knobs on the older galls, on which are borne the urediniospores and teliospores. But few sori of any kind were found on galls collected as late as November. The surface of the galls where the sori once were borne had healed over, except here and there a sorus was left which contained both urediniospores and teliospores.

The writer is placing this gall-producing form provisionally under *Neoravenelia holwayi*, since at the present time no evidence is at hand sufficient to justify separating this gall form from the typical *N. holwayi*. Further investigation and study of this rust may show that its aecial stage is not of the *Caeoma* type as is *N. holwayi*, in which case it would belong to the genus *Ravenelia* and

would be an undescribed species. As it now stands, this species parallels *Ravenelia arizonica*, both species having a leaf and a gall form; the galls of each usually bear only urediniospores, while teliospores are rarely found on the galls but usually occur on the leaves.

Type material of each of the 3 new species of *Ravenelia* described in this paper has been deposited in the Pathological and Mycological Collections of the Bureau of Plant Industry, Department of Agriculture, Washington, D.C.

OFFICE OF INVESTIGATIONS IN
FOREST PATHOLOGY
BUREAU OF PLANT INDUSTRY
ALBUQUERQUE, N.M.

ARBORES FRUTICESQUE CHINENSES NOVI. III[1]

CAMILLO SCHNEIDER

Cotoneaster (Sect. CHAENOPETALUM Koeh.) **oligocarpa,** n.sp.—Frutex latus, erectus, ad 4 m. altus; ramuli hornotini initio tomento villosulo flavescenti-cinereo adpresso obtecti, annotini satis glabrescentes, fusco-rubri, vetustiores glabri, plus minusve cinerascentes. Folia subcoriacea, partim persistentia, ovalia, obovato-elliptica vel praesertim versus apicem ramulorum ovata (in specimine florenti distinctius obovata), apice acuta et mucronulata vel satis obtusa et interdum subrotundata, basi pleraque late cuneata, 2.5–5 cm. longa et 1.2–2.5 cm. lata, superne saturate, sed ut videtur obscure, viridia, initio laxe villosula, biennia costa impressa excepta glabra, subtus modo ramulorum novellorum dense tomentosa, etiam adulta haud vel tantum in costa elevata paullo glabrescentia, in facie sub microscopio papillis distinctis non praedita, nervis lateralibus superne plus minusve impressis subtus satis prominentibus utrinsecus 8–12; petioli dense tomentosi, vix ultra 6 mm. longi; stipulae triangulari-lanceolatae, acuminatae, petiolis breviores, subtus dense tomentosae, superne glabriores. Corymbus satis densus, multiflorus, ad 4 cm. (vel ultra?) latus et ad 3.5 cm. altus, villosus, bracteis bracteolisque deciduis subulatis circ. 3 mm. longis; pedicelli 1–3 mm. longi, ut pedunculi villosi; flores albi; receptaculum ovato-turbinatum ut sepala late triangularia circ. 1–1.5 mm. longa apice glanduloso-mucronulata intus glabra satis dense tomentosulum, ad 2.5 mm. longum;

[1] Through an unfortunate coincidence, three of the species of *Mahonia* proposed by me in the previous paper (BOT. GAZ. **63**: 519–521. 1917) have been described by TAKEDA in his "Contributions to the knowledge of the Old World species of the genus *Mahonia*" (Not. Roy. Bot. Gard. Edinburgh, nos. 29, 30, January 1917). I had no knowledge of this publication until it was too late to change the names in my paper.

M. caesia Schn. is apparently the same as *M. bracteolata* Takeda, of which I have not yet seen the type or the figure, TAKEDA'S being not yet published. *M. nivea* Schn. becomes a synonym of *M. hypoleuca* Takeda; and TAKEDA is the first author of *M. philippinensis*. HENRY'S no. 10309, cited by me under *M. Alexandri* Schn., is referred by TAKEDA to his new *M. lomariifolia*, of which I have cotypes before me. I do not believe that the two species are the same, the shape and color of the leaflets being, in my opinion, too different.

petala orbicularia, circ. 2.5 mm. lata, basi unguiculata, intus pilosula; stamina 20, petalis paullo breviora, antheris ut videtur violaceis; carpidia 2, apice sparse villosa, stylis quam stamina fere longioribus stigmatibus capitatis planis. Fructus parvi, rubri, subglabri vel satis villosuli, plus minusve turbinati, 4–5 mm. longi, apice circ. 3 mm. crassi, sepalis extus villosulis incumbentibus fere clausi; pyrenia 2, obcordato-ovoidea, circ. 3.5 mm. longa et infra medium 2.5–3 mm. lata, stylum in apice vel paullo infra gerentia, ventre leviter carinata, subnitentia, dorso paullo sulcata, basi hypostylii leviter constricta, hypostylio circ. trientem dorsi occupante villosulo.

Yunnan boreali-occidentalis: in dumetis ad vias inter Ho-ching et Li-chiang-fu, alt. circ. 2600 m., 25 Septembris 1914, *C. Schneider* (no. 3070; typus in Herb. Arb. Arn. et Hb. Schneider).—Szechuan australis: ad vias in declivibus montium prope Wo-lo-ho, alt. circ. 2800 m., 13 Junii 1914, *C. Schneider* (no. 1498; foliis pro parte distinctius obovatis).

Judging by its very small fruits, this species is closely related to *C. salicifolia* Fr. which, however, may easily be distinguished by its more lanceolate and more acuminate leaves, which are more deeply furrowed and rugulose above and more glabrescent on the strongly prominent midrib and veins beneath, by its almost glabrescent fruiting inflorescences, and by the glabrous larger hypostyle. *C. salicifolia* var. *rugosa* R. and W. and var. *floccosa* R. and W. differ by the same characters of the leaves and by their larger more subglobose fruits. Its nearest relative may be *C. Harrowiana* Wils., of which I have not yet seen the fruit; but the old leaves of this species are much more glabrescent beneath. Having introduced *C. oligocarpa* into cultivation, it has to be decided by observation of living plants whether it is a good species or only a variety of *C. Harrowiana* which comes from southern Yunnan. *C. salicifolia* and its varieties, *C. Harrowiana* and *C. oligocarpa*, certainly form a group of very closely related species which may be distinguished from *C. Henryana* R. and W. and its allies by their leaves bearing no distinct papillae on the under surface, while on the leaves of *C. Henryana* the papillae are very distinct under the microscope.

Cotoneaster (Sect. CHAENOPETALUM Koeh.) **Vernae,** n.sp.—Frutex erectus, elongato-ramosus, altitudine incerto; ramuli hornotini dense cinereo- vel subflavescenti-villosulo-tomentelli, annotini plus minusve glabrescentes, fusco-rubri. Folia partim persistentia, subcoriacea, elliptico-oblonga, apice obtusa vel rotundata, basi acute vel obtuse cuneata, 2–3.5 cm. longa, 0.8–1.5 cm. lata, superne saturate viridia, subnitentia, etiam novella

tantum in costa impressa pilosa, facie plana sed tenuissime reticulata nervis non incisis, subtus dense ut ramuli tomentosa, etiam biennia tantum in costa prominente paullo glabrescentia, nervis lateralibus utrinsecus 5–7 vix vel paullo prominulis; petioli vix ad 5 mm. longi, dense tomentelli; stipulae anguste triangulari-lanceolatae, acuminatae, petiolis breviores, subglabriores. Corymbus pluriflorus, ad 3 cm. latus et 2.5 cm. longus, dense villoso-tomentosus; pedicelli 1–2 mm. longi, ut pedunculi tomentelli, bracteis bracteolisque deciduis; flores ignoti; fructus parvi, obscure rubri, turbinati vel globoso-turbinati, circ. 4 mm. longi et 3 mm. crassi, plus minusve villosuli, apice sepalis incumbentibus extus villosis fere clausi; pyrenia 2, circ. 3 mm. longa et 2.5 mm. lata, obovoidea, ventre plana, satis laevia, nitidula, dorso leviter rugulosa, stylum apice gerentia, hypostylio circ. trientem dorsi occupante villosulo.

Yunnan boreali-occidentalis: ad latera orientalia montium niveorum prope Lichiang-fu, alt. circ. 3000–3200 m., Octobri 1914, *C. Schneider* (no. 2676; typus in Herb. Arb. Arn. et Hb. Schneider).

The fruits of this species are extremely like those of *C. oligocarpa* Schn., previously described, but in its narrow elliptic obtuse leaves, which are smooth above and show very little prominent veins beneath, *C. Vernae* differs widely from all the species mentioned above. It seems to be more closely related to *C. pannosa* Fr. which, however, can easily be distinguished by its more ovate acute or shortly acuminate leaves, and by its larger fruits, the sepals of which are more erect. I am unable to identify my no. 2676 with any Chinese species hitherto described. I introduced it into cultivation (seed no. 578), and observations of living plants may give further indications of the real relationship of this apparently well marked species. It is named for my daughter Verna.

PRUNUS LATIDENTATA Koeh., var. **trichostoma,** n.var.—*P. trichostoma* Koehne in Sargent, Pl. Wils. 1: 216. 1912.—A typo non nisi sepalis intus et stylis basi distinctius pilosis differre videtur.

Szechuan australis: in regione Yen-yüan Hsien, inter viculos Ka-la-pa et Liu-ku, in sepibus, alt. circ. 3200 m., 17 Maji 1914, *C. Schneider* (no. 1210; frutex ad 2 m. altus); inter viculos Hun-ka et Wo-lo-ho, alt. circ. 3300 m., 13 Junii 1914, *C. Schneider* (no. 3520; arbuscula vel arbor ad 6 m. alta).

According to KOEHNE'S own statement, there is really no other difference between *P. latidentata* and *P. trichostoma* than the pubescence inside the sepals. So far as I can judge by the specimens before me, this character seems to be not sufficient to separate these two species. In my specimens the branchlets and pedicels are a little more hairy, and it seems to me rather difficult to decide to which of KOEHNE'S types the two numbers of mine are to be referred.

POTENTILLA ERIOCARPA Wall., var. **cathayana,** var. nov.—? *P. eriocarpa* Franchet, Pl. Delav. 211. 1889, non Wall., sensu Lehmann et Wolf; Diels in Not. Bot. Gard. Edinbgh. 7: 157. 1912, 387. 1913.—A typo a cl. Lehmanno depicto recedit foliolis omnibus sessilibus, inflorescentiis ad 3-floris, sepalis externis ovato-lanceolatis subacuminatis quam interna paullo latiora saepe distinctius acuminata vix vel paullo brevioribus.

Yunnan boreali-occidentalis: in fauce infra glaciem parvam montium niveorum prope Lichiang-fu, in rupestribus calcareis, alt. circ. 3900 m., 17 Augustii 1914, *C. Schneider* (no. 2274; typus in Herb. Arn. Arb. et Hb. Schneider; suffrutex floribus magnis luteis, ramulis floriferis 5–15 cm. altis).

According to the figure given by LEHMANN and to WOLF'S description, the typical *P. eriocarpa* Wall. has "sepala externa late elliptica obtusa vel rotundata," and the leaflets are described as "plus minusve longe petiolulata (saltem terminale)." The petals of var. *cathayana* seem also to be much more emarginate than those of the type.

Rubus (Subgen. IDAEOBATUS Focke, sect. IDAEANTHI Focke) **testaceus,** n.sp.—Frutex habitu *R. Idaei* ad 1.5 m. altus, dumeta formans; rami vetustiores teretes, aculeis paucis aculeolis sparsis vel crebris rectis armati, satis dense villosuli et glanduloso-setulosi, setulis intermixtis, partim glabrescentes et testacei; ramuli floriferi ut videtur nondum satis evoluti ad 10 cm. longi, cum petiolis pedicellisque densius griseo-villosuli et etiam glanduliferi et parce setulosi. Folia visa omnia ternata; foliola ovato-rhomboidea vel rhomboideo-orbicularia, iis *R. schizostyli* ex icone a cl. Focke in monogr. p. 206 dato satis similia, terminalia petiolo ad 1 cm. longo suffulta, maxima visa ad 3.5 cm. longa et 3 cm. lata, apice rotundata, obtusa (vel rarius in foliolis satis juvenilibus oblongioribus subacuta), lateralia subsessilia, ad 1.8 cm. longa et 1.5 cm. lata, omnia subaequaliter satis grosse dentata vel inaequaliter dentato-serrata, sublobulata, superne satis flavo-viridia, laxe vel initio densius subadpresse hirto-pilosa et glandulosa, subtus vix discoloria, facie glabriuscula, in costa nervisque lateralibus utrinsecus (3–) 4 (–5) hirta et plus minusve glandulosa; petioli ad 2 cm. longi; stipulae lineares ad 6 mm. longae, praesertim extus villosae et glanduliferae. Flores axillis foliorum ex parte quasi ad bracteas reductorum singuli, apice ramulorum floriferorum pseudoracemas ad 6-(vel pluri-?) floras formantes, rubri, iis *R. triphylli* similes, circ. 1.5 cm. diametientes; pedicelli ad 15 mm. longi, medio saepe

bractea stipulis simillima instructi; calyx externe modo pedicellorum villosulus, glanduliferus et parcissime setulosus, sepalis lanceolatis acuminatis margine albo-villosis circ. 7 mm. longis patentibus intus basi glabrioribus; petala oblonga vel satis anguste obovato-oblonga, versus apicem acutiusculam undulato-marginata, basim versus longe cuneata, intus sparse pilosa, demum ut videtur patentia, sepalis subaequilonga et ultra medium circ. 3–3.5 cm. lata; stamina in flore ut videtur erecto-patentia, circ. 70–75, filamentis glabris longioribus petalis subaequilongis; carpophorum pilosum; carpidia circ. 30, 4.5–5 mm. longa, stylis glabris, ovariis ima basi pilosis et dorso pilis parcis praeditis; discus glaber. Fructus ignoti.

Szechuan australis: in regione Yen-yüan Hsien, inter viculos Ka-la-pa et Liu-ku, alt. circ. 3500 m., 17 Maji 1914, *C. Schneider* (no. 1269; frutex ad 1.4 m. altus, dumeta formans, foliis valde juvenilibus); eodem regione, ad viam inter Liu-ku et Kua-pie, alt. circ. 2800 m., 19 Maji 1914, *C. Schneider* (no. 1213; flores rubri).—Yunnan boreali-occidentalis: in regione Yung-ning, versus pagum Mu-ti-chin, alt. circ. 2800 m., 23 Junii 1914, *C. Schneider* (no. 3894; typus in Herb. Arb. Arn. et Hb. Schneider).

Judging by the shape of the leaves, this species seems to be very similar to *R. schizostylus* Lév., which I know only from the figure given by FOCKE in his Mon. Gen. Rubi Prodr. in Bibl. Bot. **72**: 206. *fig. 83.* 1911; but according to the description of the author this Corean species differs widely in having "rami rubescentes glabri . . . . foliola . . . . subtus cinerea . . . . pilis adpressis albis." *R. mesogaeus* Focke, l.c. 204. *fig. 82*, which is found in Hupeh and Szechuan, has white or pink flowers, and is otherwise extremely different. Another species to which *R. testaceus* may be related is *R. kanayamensis* Lév. and Van. in Bull. Soc. Bot. France **53**: 549. 1906 et apud Focke, l.c. 205, from Japan, of which the leaves are described as "in utraque pagina viridia et parce pilosa," but it has an "inflorescentia laxe effusa," and, according to FOCKE's statement, "revocat *R. id.* subspec. *strigosum*," the shape of the leaves of which is entirely different. The specific name of the new species refers to the pale brick red color of the older glabrescent branches.

ROSA MAIREI Lév., var. **plurijuga,** n.var.—A typo praecipue recedit foliis 5–6-jugis, foliolis etiam superne plus minusve dense villosulis.—Fructus plantae typicae incogniti, in varietate magni, rubri, ad 15 mm. crassi et 18 mm. longi (sepalis persistentibus exclusis), obovato-globosi, praesertim ad apicem tomentelli, ceterum glabri, basi subsensim in pedicellum contracti, apice sepalis utrinque dense villosulo-tomentellis lanceolato-triangularibus acuminatis ad 15 mm. longis basi circiter 6 mm. latis coronati,

pedicelli ad 18 mm. longi, plus minusve tomentelli, apice excepto non incrassati.

Yunnan boreali-occidentalis: in declivibus herbosis calcareis montium Tsang prope Tali-fu, alt. circ. 2800 m., Augusto 1914, *C. Schneider* (no. 2526; typus in Herb. Arb. Arn. et Hb. Schneider).

This variety agrees well with typical *R. Mairei* Lév. except that the leaves have 5–6 pairs of leaflets instead of only 2–4 pairs. Unfortunately the fruits of the type are still unknown. REHDER and WILSON in Sargent, Pl. Wils. **2**: 344. 1915, say that *R. Mairei* "is probably nothing more than a very hairy and small-leaved variety of *R. omeiensis* Rolfe." In my opinion, it seems much more closely related to *R. sericea* Ldl. which, however, comes very near *R. omeiensis*. The new variety may be identical with the true *R. sericea*, f. *pteracantha* Franchet in Pl. Del. 220. 1889=*R. sericea* Crépin in Bull. Soc. Roy. Bot. Belg. **25**: 9. 1886, ex parte, quoad no. 861 Delavayi, which he describes as having "folia majuscula utraque facie sericeo-tomentella," but he does not mention the number of the leaflets neither does CRÉPIN. FRANCHET'S f. *pteracantha*, however, is not identical with *R. sericea* var. *pteracantha* in Gard. Chron. III. **28**: 260. *figs. 98, 99*, 1905; and in Bot. Mag. **134**: *pl. 8218*. 1908, which is the same as *R. omeiensis* f. *pteracantha* R. and W. in Sarg., Pl. Wils. **2**: 332. 1915.

The typical *R. omeiensis* Rolfe is well characterized by its 9–13-foliolate leaves, the leaflets of which are entirely glabrous or hairy only on the midrib beneath, and by the distinctly thickened and colored (yellow or red) footstalks of the ripe fruits (see Bot. Mag. **138**: *pl. 8471*. 1912); but there are certain hairy forms with almost subsessile fruits and fewer leaflets which come very near to *R. Mairei* as well as to *R. sericea*. The type of *R. sericea* as represented by LINDLEY in his Rosac. Monogr. 105. *pl. 12*. 1820, has 7–11 leaflets which are "green and naked above, paler, with the rib and the principal veins silky beneath." We certainly need a careful study of all the forms of these 3 species which, after all, seem to be so closely connected by intermediate forms that they may have to be united under *R. sericea* which we have to study as CRÉPIN said, "au point de vue des variations que peut éprouver un type dans le revêtement de ses axes et de ses feuilles." By WILSON, FORREST, and myself many forms have been introduced into cultivation, so that we shall be able to judge the value of the different characters presented by the leaves, fruits, and branchlets by the behavior of living plants.

Rosa (Sect. CINNAMOMEAE DC.) **atroglandulosa,** n. sp.—Frutex latus erectus, ad 1.5 m. altus; rami purpurascentes glabri, aculeis satis sparsis vel in ramulis floriferis tantum infrastipularibus rectis acicularibus basi subito plus minusve dilatatis ad 8–9 mm. longis flavis muniti; turiones non visi. Folia satis crassa, chartacea, 5-foliolata, petiolo incluso 5–8 cm. longa; foliola breviter petiolulata, ovalia, ovato-elliptica, rarius obovalia, apice satis obtusa

vel breviter acuta, basi plus minusve rotundata, rarius late cuneata, lateralia inferiora minora (13–) 15–22 mm. longa, (8–) 10–15 mm. lata, superiora majora ad 3.2 cm. magna, terminalia superioribus plus minusve aequalia sed saepe paullo latiora, margine dupliciter inaequaliter glanduloso-serrata (sublobulata) dentibus majoribus mucronulatis porrectis dorso denticulas 1–3 gerentibus, superne viridia, in sicco leviter glaucescentia, laevia, glabra (interdum sparsissime glanduloso-pilosa), subtus viridescentia, dicoloria, in costa et etiam partim in nervis lateralibus utrinsecus 5–8 paullo prominulis satis rectis plus minusve pilosa et etiam ut in facie pilis glanduliferis crebris conspersa (oculo nudo quasi nigro-punctata), rete nervillorum subvisibili; petioli 2–3.5 cm. longi, ut rhachis plus minusve dense villosuli, stipitato-glandulosi et setis aculeolisque sparsis muniti; stipulae satis evolutae, ad medium adnatae, 10–13 mm. longae, auriculis latis acuminatis, margine dense glanduloso-ciliatae, ceterum ut folia pilosa et glandulifera. Flores kermesini, suaveolentes, circ. 3 cm. diametientes, solitarii vel 2–3 apice ramulorum ad 8 cm. longorum terminales; pedicelli 10–12 mm. longi, basi bracteis ovatis vel late ovatis apice subito acuminatis ad 12 mm. longis et 8–9 mm. latis dense glanduloso-ciliatis suffulti, glabri, interdum fere nudi sed plerique crebre stipitato-glandulosi; receptaculum ellipsoideo-oblongum, glabrum, nudum; sepala ovato-oblonga, extus glabra vel interiora versus marginem tomentella, intus tomentosula, eglandulosa, post florationem reflexa; alabastra ovata, obtusa; petala late obovata, emarginata, ad 2 cm. longa et 1.7 cm. lata; stamina numerosa, antheris luteis ovalibus; styli liberi, circ. 5 mm. exserti, staminibus longioribus vix breviores, villosi. Fructus ignoti.

Szechuan australis: inter urbem Yen-yüan Hsien et viculum Hun-ka, ad vias, alt. circ. 2600–2800 m., 11 Junii 1914, *C. Schneider* (no. 1484; typus in Herb. Arb. Arn. et Hb. Schneider).

This species seems to me most closely related to *R. Sweginzowii* Koehne (see figure in Fedde, Rep. Spec. **11**: 531. *fig. 3*) and R. *setipoda* Hemsl. and Wils. (see Bot. Mag. **140**: *pl. 8569*), which may easily be distinguished in having 7–9 leaflets and a different kind of wide-based prickles. *R. atroglandulosa* seems to be well marked by the frequent stipitate dark glands on the under surface of the leaves and the rather long exerted styles. I cannot refer it, even as a variety, to any of the species of this section enumerated by A. REHDER in Sarg., Pl. Wils. **2**: 339. 1915.

ROSA SOULIEANA Crép. var. **yunnanensis,** var. nov.—*R. moschata* var. *yunnanensis* Focke in Not. Bot. Gard. Edinbgh. **5**:69. 1911, nom. nud., non Crépin apud Franchet; DIELS, l.c. **7**:124. 1912 et 394. 1913, nom. nud.; *R. Soulieana* R. and W. in Sarg., Pl. Wils. **2**:314. 1915, quoad synon. Fockii et specim. Forrestii, non Crépin.—A typo recedit rhachi foliorum et costa foliolorum subtus puberula, pedicellis receptaculisque minute flavo-glanduloso-pilosis et etiam interdum pilosulis.

Szechuan australis: inter viculos Wo-lo-ho et Hu-ma-ti ad viam versus Yung-ning, alt. circ. 2800 m., 14 Junii 1914, *C. Schneider* (no. 1549; frutex ad 2.5 m. altus, patenter dense ramosus, floribus albis odoratis).

The main difference between the type and this variety seems to be the fine pubescence of the rhachis and of the midrib of the under side of the leaflets, which is not always present on the pedicels and receptacles. These are more or less covered with a short, yellowish, glandular pubescence which I find also on a cultivated specimen from VILMORIN'S fruticetum, Les Barres. VILMORIN'S plant, probably, came from the type plant in the Jardin des Plantes in Paris. The shape of the leaflets, which are described by FRANCHET as "courtes, ovales et plus ou moins arrondies, à base arrondie, obtuses- arrondies au sommet, plus rarement très brusquement mucronées," varies to a certain degree, and especially the leaves of FORREST'S no. 2370 from Lichiang, which is the type of var. *yunnanensis* of Focke, are rather acute at both ends.

VIBURNUM CYLINDRICUM Ham., var. **crassifolium,** n. var.—*Viburnum crassifolium* Rehder in Sarg., Pl. Wils. **2**:112. 1913.—A typo cum varietate ut videtur formis intermediis conjuncto differt praecipue inflorescentiis plus minusve vel satis dense pubescentibus.

Szechuan australis: in regione Yen-yüan Hsien versus occidentem inter viculos Hu-ma-ti et Wo-lo-ho, alt. circ. 2800–3000 m., 14 Junii 1914, *C. Schneider* (no. 1552; arbuscula vel arbor ad 6:0.4 m.).—Yunnan boreali-occidentalis: in dumetis inter viculos Pi-ji et Pao-to versus Yung-ning, alt. circ. 2400 m., 25 Junii 1914, *C. Schneider* (no. 3508; frutex ad 3 m. altus); in dumetis ad pedem orientalem montium niveorum prope Lichiang-fu, alt. 2900–3200 m., 29 Julii 1914, *C. Schneider* (no. 2034; frutex 2–3 metralis); eodem loco, Octobri 1914, *C. Schneider* (no. 3212).

Regarding the size of the leaves and the sparser pubescence of the inflorescences, these specimens are intermediate between the type of *V. crassifolium* Rehd., collected by A. HENRY in southern Yunnan near Mengtsze (no. 9797), and the typical *V. cylindricum* Ham. to which I refer the following numbers of my own collections: Szechuan australis: in regione Yen-yüan Hsien, in silvis prope Liu-ku, alt. 3000 m., 19 Maji 1914 (no. 1315; frutex ad 2 metralis);

prope Kua pie, alt. circ. 3000 m., 21 Maji 1914, (no. 1345; frutex vel arbor, 3–6 metralis); in regione Hua-li, in dumetis declivium ad flum. Yalung, alt. 2300 m., 30 Maji 1914 (no. 1395).

VIBURNUM CALVUM Rehd., var. **puberulum,** n. var.—A typo praecipue recedit: ramulis hornotinis et saepe annotinis biennesque et etiam inflorescentiis plus minusve puberulis.—Fructus atrocyanei, nitiduli, ovato-globosi, circ. 5 mm. longi et 4 mm. crassi, iis *V. propinqui* similes sed minus distincte apiculati; semina ovoideo-globosa, ventre leviter sulcata, albumine ruminato.

Szechuan australis: inter Hoh-si et Yen-yüan Hsien prope pagum Loma-pu, in dumetis montium, alt. circ. 2200 m., 9 Maji 1914, *C. Schneider* (no. 1146; frutex virgultus, 1.5–2 m. altus, floribus albis, fructibus atrocyaneis); in regione Kua-pie, in declivibus dumosis calcareis montium, alt. circ. 3000 m. 20 Maji 1914, *C. Schneider* (no. 1325; typus in Herb. Arn. Arb. et Herb. Schneider; frutex sempervirens, 1–1.5 m. altus, fructibus nitidis nigris).

According to the shape and the nervation of the leaves, and to the size of the inflorescence, this form is very similar to the typical *V. calvum* Rehd. from southern Yunnan, of which the fruits are not yet known. The fruits I collected are about the same as those of *V. propinquum* Hemsl. which, however, can easily be distinguished by its 3-nerved leaves.

There is another very interesting species I found in Yunnan boreali-occidentalis: inter Hoching et Teng-chuan, in silvis apertis prope Sung-queh versus angustias montium, alt. circ. 3200 m., 29 Sept. 1914 (no. 2873; frutex 3-metralis). The shape of the ovate-oblong or oblong-elliptic leaves, which measure up to 8 cm. in length and 2.8 cm. in width, is similar to those of *V. propinquum*, but they are not distinctly acuminate and not 3-nerved at the base, but have the same nervation as *V. calvum*. The fruiting corymbs are small, and bear only a few fruits, which, unfortunately, are not yet fully ripe. They are almost globose, and about 5 mm. in diameter. I cannot refer this form to any species hitherto described from China, but I believe it is very near or the same as *V. atrocyanea* (sic!) C. B. Clarke apud Hook. and Thom., Fl. Brit. Ind. 3:7. 1880 from the Mishmi Mountains in Bhutan, which I know only from the rather insufficient description of the author.

ARNOLD ARBORETUM
JAMAICA PLAIN, MASS.

BRIEFER ARTICLES

ANELSONIA, A NEW GENUS OF THE CRUCIFERAE

As GREENE remarked long ago, the so-called natural families, as Umbelliferae, Labiatae, and Cruciferae, contain relatively few natural genera, and perhaps in no group of plants are generic limitations harder to define than within some sections of the Cruciferae. Consequently, there have often been included under one generic name plants that in point of fact bear little real relationship to one another. The genus *Parrya*, as it has been treated by many recent authors, furnishes, we believe, an example of this misinterpretation of generic limitations. This genus was drawn by BROWN to include several low scapose perennials of the far North, all characterized by showy purple-red flowers and glabrous (or hirtellous with simple hairs) foliage. In 1891 GREENE (Fl. Fran. 1:253) referred to *Parrya*, *Hesperis Menziesii* Hook., a plant previously made the type of a new genus by NUTTALL (T. and G., Fl. N. Amer. 1:89. 1838) under the name *Phoenicaulis cheiranthoides* Nutt., and possessing much the same aspect as the species included by BROWN in his genus, but with the foliage whitened by a thick covering of branching and stellate hairs. A critical study and comparison of this plant with the typical members of *Parrya* has disclosed the fact, however, that technical but readily discernible differences other than the character of the pubescence exist between *Parrya* and *Phoenicaulis*. The more important of these are the lack in the latter of the conspicuous network of superimposed fibers that characterize the septum of *Parrya*, the absence of the loose epidermis so prominent about the seeds of the latter genus, the remarkably tortuous areolae, tortuous in none of the species of *Parrya*, and the nearly entire and capitate stigma. The value of characters of this type for the proper delineation of genera in the Cruciferae has been proved by PRANTL in his careful synopsis of the group in *Nat. Pflanzenfamilien*, where he retains NUTTALL'S genus.

It appears, therefore, that *Phoenicaulis* is amply distinct from *Parrya;* but, as we have already suggested, the Cruciferae as a natural family is composed of many groups, the differentiation of which has occurred within comparatively narrow limits. Such groups, possibly remotely related, may have analogous forms, and then their true relationships are apt to be lost by the systematist, particularly if he bases his classification

on vegetative characters or places too much dependence upon the often fickle "aspect." Circumstances of this nature doubtless contributed largely to the treatment by NELSON (Proc. Biol. Soc. Wash. **18**:187. 1905) of *Phoenicaulis Menziesii* as a species of *Arabis*, a disposition that was adopted later by NELSON and MACBRIDE (BOT. GAZ. **55**:374. 1913). It must be admitted that the arguments in favor of this treatment are far from weak; on the other hand, the highly technical nature of the characters to be considered in the proper definition of groups in a natural family must be borne in mind, and PRANTL has used to advantage, in "keying" *Phoenicaulis* and *Arabis*, the type of characters that furnish the best contrasts between *Parrya* and *Phoenicaulis*. The very possibility of considering *P. Menziesii* as an *Arabis* becomes, therefore, a strong argument for its retention as a genus distinct from both *Parrya* and *Arabis*.

We now come to a consideration of the plant which prompted these observations. This plant was described by GRAY (Proc. Am. Acad. **6**:520. 1866) from meager material that was far past condition as *Draba eurycarpa*, and recently has been redescribed as *Parrya Huddelliana* A. Nels. (BOT. GAZ. **54**:139. 1912). Here again we have an instance of the similarity of genera in this family, especially as regards vegetative characters. This plant would not seem at all out of place in *Draba* were aspect the only criterion we had to judge it by; and indeed the original specimen consists only of two small plants which are so mature that the seeds have all fallen. But upon examination of complete material it becomes obvious that GRAY'S species is allied to *Parrya* and *Phoenicaulis*. It is not satisfactory, however, to refer it to either of these genera. The branching pubescence, the inconspicuous white flowers, the subentire stigma, the broadly ovate-lanceolate pods, and the nearly membranous septum are some of the characters that forbid its reference to *Parrya*. The loose cellular testa about the seeds, the not at all tortuous areolae, and the inconspicuous flowers are also characters in direct contrast to those of *Phoenicaulis*. Moreover, there is the unique habit which suggests *Draba* rather than either of the genera to which it is most nearly related, but consideration of it as a *Draba* (to mention one outstanding feature) is out of the question because of the singular seed coat. Although this is suggestive of the seed coat of *Parrya*, it is of a different quality and is not winged.

Now in the proper generic allocation of these plants consideration must be given only to the value of the characters indicated for purposes of generic definition. The characters themselves are obviously definite

and distinctive; and it seems to us that there is only one possible interpretation of the problem which will conform to what experience has shown to be the logical and practical treatment of cruciferous groups. In pursuance of this view it becomes necessary to consider *Draba eurycarpa* as representing a generic type intermediate in some respects to *Parrya* and *Phoenicaulis*, and more closely related to these genera than to any others, but at the same time more distinct from either of these than they are from each other. In recognition of the notable work of AVEN NELSON, we propose that this genus bear the name *Anelsonia*.

The distinguishing characters of these related genera may be summarized as follows:

Pods ovate-lanceolate, mid-vein obscure; septum merely membranous; seeds with a loose cellular epidermis, not margined, areolae not tortuous; pubescence of branching hairs; petals white, little exceeding the pubescent sepals; stigma subentire. . . . . *Anelsonia*

Pods narrowly ensiform or more or less attenuate at both base and apex; mid-vein evident; seeds smooth without loose epidermis or, if this is present, more or less margined; petals usually red purple, much exceeding the glabrous sepals.

Pods more or less attenuate at both base and apex; septum bearing a conspicuous network of superimposed fibers; seeds with a loose cellular epidermis usually more or less winged, areolae not tortuous; pubescence wanting or the hairs simple; stigma lobed. . . . . *Parrya*

Pods narrowly ensiform; septum merely membranous; seeds smooth without loose epidermis, areolae remarkably tortuous; pubescence branching and stellate; stigma subentire. . . . . *Phoenicaulis*

Anelsonia, gen. nov.—Siliqua compressa ovato-lanceolata costa media inconspicue, septo membranaceo-hyalino, evanido, stigmati fere simplici. Semina 2-seriata, testa cellulosa. Sepala plus minusve pubescentia. Petala brevia.—Herbae humiles, alpinae, subcaespitosae et scapigerae, pube brevi furcata vel ramosa canae. Folia integerrima. Flores inconspicui, albi.

Anelsonia eurycarpa (Gray), comb. nov.—*Draba eurycarpa* Gray, Proc. Am. Acad. **6**:520. 1866; *Parrya Huddelliana* A. Nels. BOT. GAZ. **54**:139. 1912.

In alpine rock slides, Idaho to California.—IDAHO: Mackay, Custer County, July 31, 1911, *Nelson* and *Macbride*, no. 1466; Lost River Mountains west of Clyde, Blaine County, July 10, 1916, *Macbride* and *Payson*, no. 3128; CALIFORNIA: peak near Sonora Pass, 1863, *Brewer*, no. 1909.—J. F. MACBRIDE AND E. B. PAYSON, *University of Wyoming*.

CURRENT LITERATURE

BOOK REVIEWS

Researches in plant physiology

ATKINS[1] has written an interesting little book, the aims of which can best be expressed by quotations from the preface. "The general aim of the book is to present to senior students and investigators the results of recent work in a few of those branches of plant physiology which are at present attracting attention." "By such a presentation of portions of the science which are still in a state of rapid growth, it is hoped that further investigation will be stimulated. The choice of material by the author was, to a considerable degree, influenced by his familiarity with certain subjects of general interest, portions of which are being studied experimentally by the staff of the School of Botany, Trinity College, Dublin. Upon these, rather than upon other researches of equal or greater importance, he has felt qualified to write, on account of his first-hand knowledge of many of the methods employed. A small amount of hitherto unpublished work has also been included."

A list of the chapter headings gives an idea of the content of the book: I. The carbohydrates of the angiosperm leaf in relation to photosynthesis; II. Methods of estimating carbohydrates in plant extracts; III. The carbohydrates of the Thallophyta and Bryophyta in relation to photosynthesis; IV. The pectic substances; V. Osmotic pressure in plants; VI. The osmotic equilibrium between the cell and its surroundings; VII. The permeability of protoplasm; VIII. The permeability of organic membranes other than protoplasm; IX. The magnitudes of osmotic pressures and electrical conductivities in plants, and the factors which influence them; X. Osmotic pressure in relation to plant distribution, morphology, and cell division; XI. The functions of the wood; XII. The plant oxidases; XIII. The oxidases in relation to pigmentation, and the anthocyan pigments; XIV. The oxidases in relation to plant pathology and to technology.

As compared with a treatise on plant physiology, the book of course appears patchy, but this is an outgrowth of the aim, and is by no means an unfavorable criticism of the work. It is written in a most interesting as well as thoroughly scientific manner. On reading it one is convinced that it will attain its aim of stimulating research along many of the lines treated.—WM. CROCKER.

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[1] ATKINS, W. R. G., Some recent researches in plant physiology. pp. xi+328. London: Whittaker Co. 1916.

NOTES FOR STUDENTS

Taxonomic notes.—BURT[2] has described a new species of *Pistillaria* (*P. Thaxteri*) which he records as the smallest known hymenomycete. It was collected in Connecticut, and is so minute that the "fructifications are not visible to the naked eye unless rendered so by special illumination and background." The fructifications were observed scattered on the surface of very rotten wood, "merely gregarious, not united into clusters," and as many as 115 were counted on an area 2×0.5 cm. The fungus is remarkable not only as the smallest known "toadstool," but also for its extreme simplicity of structure.

FERNALD[3] has described a new species of *Juncus* (*J. pervetus*) from Cape Cod, resembling *J. Roemerianus* in many particulars. It is stated that this new species "is one of the many remarkable species of world-wide affinities which are being discovered so frequently on the coastal area of southern New England and southeastern British America."

GATES[4] has had occasion to investigate *Trillium* in connection with his work in genetics, and has been impressed with the great variability of the genus in certain organs. In attempting to delimit the species, he recognizes 31 species with 9 varieties. *T. venosum* is described as a new species from Idaho, and new varieties are described in *T. luteum*, *T. lanceolatum*, *T. grandiflorum*, and *T. ovatum*. The published records of variation in the genus are brought together, and their number is remarkable. The author suggests that the genus *Paris* has been derived from the *T. erectum* group, and that *Medeola* has also come from *Trillium*.

GREENMAN,[5] in continuing his studies of *Senecio*, has presented § LOBATI, comprising 16 species, 4 of which are described as new.

HOWE and HOYT,[6] in studying a small collection of algae obtained through dredging operations on August 11, 1914, in water on a reef about 23 miles off shore from Beaufort, discovered 7 new species belonging to the following genera: *Microchaete*, *Derbesia*, *Phaestroma*. *Erythrocladia* (2), *Acrochaetium* (2). The collection also contained 2 species previously known from Europe only, namely, *Streblonema solitarium* and *Elachristea stellulata*.

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[2] BURT, E. A., *Pistillaria* (subg. *Pistillina*) *Thaxteri* Burt, n.sp. Ann. Mo. Bot. Gard. **3**:403–406. 1916.

[3] FERNALD, M. L., A new *Juncus* from Cape Cod. Rhodora **19**:17–20. 1917.

[4] GATES, R. R., A systematic study of the North American genus *Trillium*, its variability, and its relation to *Paris* and *Medeola*. Ann. Mo. Bot. Gard. **4**:43–92. *pls. 6–8*. 1917.

[5] GREENMAN, J. M., Monograph of the North and Central American species of the genus *Senecio*. Part II. Ann. Mo. Bot. Gard. **4**:15–36. *pl. 4*. 1917.

[6] HOWE, M. A., and HOYT, W. D., Notes on some marine algae from the vicinity of Beaufort, North Carolina. Mem. N.Y. Bot. Gard. **6**:105–123. *pls. 11–15*. 1916.

MACKENZIE,[7] in continuation of his studies of *Carex*, has presented the "Californian representatives of the OVALES." The list includes 25 species, 15 of which are described as new.

ROBINSON[8] has published a detailed monograph of the American genus *Brickellia*. The need of it, the author remarks, "presents no unusual condition among the larger genera of the Compositae." The 91 species, 11 of which are new, are grouped in 9 sections. The systematic presentation is preceded by a full discussion of the diagnostic value of the characters used.

RYDBERG,[9] in continuation of his studies of the Rosaceae, has investigated the species of *Rosa* occurring in California and Nevada. He recognizes 34 species, 12 of which are described as new.

TIDESTROM[10] has described a new *Allium* (*A. platyphyllum*) from the Wallowa National Forest of Oregon.—J. M. C.

Effect of carbon dioxide on respiration.—KIDD[11] has studied the effect of various concentrations of carbon dioxide on the rate of anaerobic and aerobic respiration of seeds of peas with testas both intact and removed. The work is marked by brilliancy of design, and in the main of execution. In concentrations of CO_2 ranging from 0 to 50 per cent, the depressing effect on anaerobic respiration is proportional to the square root of the concentration. As the concentration rises above 50 per cent, the depressing effect falls more and more behind the square root of the concentration. Carbon dioxide also depresses aerobic respiration when measured either by oxygen consumption or CO_2 production. In the latter case the concentration effect is similar to that in anaerobic respiration. When oxygen is deficient, CO_2 has no depressing effect upon the oxidation phase. It is assumed that the primary anaerobic phase is then progressing fast enough not to limit the secondary aerobic phase of respiration, and that it is only the anaerobic phase that CO_2 depresses. Only the so-called floating respiration of BLACKMAN (respiration of storage carbohydrates, fats, and proteins) and not protoplasmic respiration (respiration still occurring in starving tissue) is thus depressed. The work throws considerable light upon the mechanism of respiration.

In work of this sort one should be sure that the cultures are sterile and that the anaerobic CO_2 production is that of the seeds and not of organisms growing

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[7] MACKENZIE, K. K., Notes on *Carex*. XI. Bull. Torr. Bot. Club **43**:601–620. 1916.

[8] ROBINSON, B. L., A monograph of the genus *Brickellia*. Memoirs Gray Herb. I. pp. 151. *figs. 95*. 1917.

[9] RYDBERG, PER AXEL, Notes on Rosaceae. XI. Bull. Torr. Bot. Club **44**:65–84. 1917.

[10] TIDESTROM, IVAR, *Allium platyphyllum*, sp. nov. Torreya **16**:242. 1916.

[11] KIDD, FRANKLIN, The controlling influence of carbon dioxide. Part III. The retarding effect of carbon dioxide on respiration. Proc. Roy. Soc. B **89**:136–156. 1916.

on them. While the author speaks of sterilizing the seeds with bromine, he says nothing about making cultures to assure that they are sterile. Many authors find it difficult to sterilize seeds without killing them. This is specially true of those with open micropyles. From the first two papers of the series, KIDD reemphasizes his conception that the dormancy of "moist seeds" is due to the anesthetic action of carbon dioxide which is held in by seed coats. If this be the cause of dormancy in any imbibed seeds, it is limited in its application. It does not apply to seeds which have a rest period during which the embryo is developing; to seeds like *Alisma* and *Amaranthus*, in which the swelling contents do not have sufficient pressure to break the coats; or to seeds like *Crataegus*, in which the embryos are dormant when naked.[12] He has by no means proved that this holds even for forms forced by increased oxygen pressure (*Xanthium* and others). His conception implies that the coats of these seeds are very slightly permeable to CO_2. In the elementary course in plant physiology in Hull Botanical Laboratory, we used for years various seed coats and the epidermis of various leaves to show that moist plant membranes are relatively very permeable to CO_2 in contrast to oxygen and nitrogen. KIDD's assumption concerning CO_2 and dormancy of seeds, therefore, even under limited application, cannot be considered more than an hypothesis without a study of the permeability character of the seed coats to CO_2 and other gases.—WM. CROCKER.

Vegetation of South Africa.—In a region where climate differs strikingly over areas of comparatively small size, there is usually a corresponding diversity of vegetation. Apparently such diversity is displayed to a remarkable degree in South Africa, as seen in the recent studies by BEWS. In his earlier papers, reviewed in this journal,[13] a general account of the vegetation of Natal was given and a more detailed study of some areas within its limits. In his latest article BEWS[14] has sketched the vegetation of a wider area and has begun the study of its succession. The condition of Table Mountain is perhaps typical of the broader area, showing a precipitation upon the western side of 60–75 cm. annually and resulting sclerophyllous scrub communities, while upon the eastern slopes the precipitation is doubled and a rather mesophytic forest results. The former characterizes the southwestern region of the Cape and passes from a fell field with an open stand of grasses, Crassulaceae, Compositae, and dwarf Ericaceae, to a heath dominated by *Blaeria ericoides*, a South African heather, or by a variety of dwarf shrubs in which species of *Protea*, *Erica*, *Rhus*, *Polygala*, and many less familiar genera, along with many bulbous monocotyledons, are conspicuous.

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[12] CROCKER, WM., Mechanics of dormancy in seeds. Amer. Jour. Bot. **3**:99–120. 1916.

[13] BOT. GAZ. **59**:68–69. 1915.

[14] BEWS, J. W., An account of the chief types of vegetation in South Africa, with notes on the plant succession. Jour. Ecol. **4**:129–158. 1916.

A related formation of higher growth is the "macchia," which in some regions succeeds the heath. In it the Ericaceae become less abundant with the increase in size of the woody plants, but such genera as *Protea* and *Rhus* have more representatives, while associated with them are species of *Olea*, *Celastrus*, *Leucadendron*, and many other genera.

On the southeastern slopes facing the Indian Ocean, the greater summer rainfall produces a mesophytic forest, often dominated by *Podocarpus* or by *Rhus longifolia* and *Albizzia fastigiata*.

Grassland, much of it interspersed with scattered trees or shrubs, known variously as *Acacia* veld, *Protea* veld, or bush veld, extends through much of Natal, Transvaal, and Rhodesia. The tree veld becomes increasingly arid toward the west and includes much of Great Namaqualand and Damaraland. Northward the vegetation becomes more luxuriant, passing to rich grasslands with large trees of the baobab, *Adansonia digitata*, and of *Copaifera mopane* in Angola.

In dry river valleys of Natal and elsewhere, a rather rich scrub formation is found, characterized by tree species of *Euphorbia*, *Aloe*, and *Mesembryanthemum*, and succulent or semisucculent lianas, in addition to the more woody shrubs and trees.

Finally, there is the Karroo with a rainfall of 8–35 cm., and a vegetation of dwarf shrubs, leaf and stem succulents, bulbous plants, a few grasses, and some annuals. BEWS is inclined to class this with the grassland rather than with the desert. He finds, in fact, that there is little true desert in South Africa, the so-called "Kalahari desert" also being more truly veld or grassland.—GEO. D. FULLER.

Effect of fungi on fruits.—HAWKINS[15] has studied the effect of the brown-rot fungus upon the chemical composition of the peach, and CULPEPPER, FOSTER, and CALDWELL[16] have made a similar but more complete study of the changes in the apple during decay by the black-rot fungus. *Sclerotinia cinerea* increases acidity of the peach during decay. Among the carbohydrates the pentosans are not attacked; the alcohol-insoluble portion which reduces Fehling's solution after being hydrolyzed with dilute hydrochloric acid is slightly decreased; and the total sugar content is much decreased. The sucrose practically disappears during decay; its inversion occurs more rapidly than the resulting reducing sugars are used by the fungus. As a result, the percentage of reducing sugars in the decaying fruit is greater than in the sound fruit, although the total sugar content is less.

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[15] HAWKINS, LON A., Some effects of the brown-rot fungus upon the composition of the peach. Amer. Jour. Bot. 2:71–81. 1915.

[16] CULPEPPER, CHARLES W., FOSTER, ARTHUR C., and CALDWELL, JOSEPH S., Some effects of the black-rot fungus, *Sphaeropsis malorum*, upon the chemical composition of the apple. Jour. Agr. Research. 7:17–40. 1916.

In the case of the apple, the lipoids are attacked and decreased, but later a large amount of lipoid is constructed in the fungus itself. Non-protein nitrogen of the apple is converted into protein nitrogen of the parasite, decrease of the former paralleling increase of the latter; but some nitrogen loss results from complete decomposition of nitrogenous compounds with liberation of ammonia. The lipoid phosphorus and protein phosphorus of the apple are first broken down into soluble form, and then reconstructed into protein phosphorus within the parasite. The sugars decrease rapidly as the disease proceeds. The disaccharides are used much less rapidly and completely than the monosaccharides. The starch content remains unchanged. Acidity decreases, for the malic acid of the apple is decomposed without the formation of any other acids by the organism, and a large amount of alcohol is formed from soluble carbohydrates. The authors claim a fairly complete statement of the chemical differences between sound and black-rot diseased apples.—CHARLES A. SHULL.

Tropical vegetation.—In a botanical travelogue, GLEASON[17] has described in a semi-popular way so many phases of vegetation as to make his series of articles an excellent one for visualizing the diversity and luxuriance of tropical forests. Japan with its intensive cultivation of all available land has so little natural vegetation that it becomes insignificant compared with the Philippines. Here the reader is guided through a forest remarkable for luxuriance and rapidity of growth, and made acquainted with many lianas, epiphytes, and strangling figs or "baletes," without losing sight of the stratification of tree growth. Interruptions of the forest growth made by the natives in their attempts at agriculture are seen in the rapid reforestration of the "parangs," or when fire has intervened in the grassy "cogons." Among other matters of botanical interest is the action of volcanoes, like that of Taal, in destroying vegetation and thus furnishing a splendid field for the study of plant reestablishment and succession.

At Java the Botanic Garden of Buitenzorg with its 16,000 species of plants and the less known but not less interesting economic garden were visited. In the latter collections of such different rubber plants as *Ficus*, *Hevea*, *Castilloa*, and *Manihot* growing side by side seem to abound. The mountain garden at Tjibodas was visited also and the beauties and advantages of these collections of tropical plants are pointed out. A similar visit to the garden at Peradeniya and excursions to examine various types of vegetation upon the island of Ceylon complete the tour.—GEO. D. FULLER.

Potamogeton.—HAGSTRÖM[18] has published an elaborate monograph on *Potamogeton*, in which the classification is based largely upon anatomical

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[17] GLEASON, H. A., Botanical sketches from the Asiatic tropics. I. Japan; II. Philippines; III. Java; IV. Ceylon. Torreya **15**:93–101, 117–133, 139–153, 161–175, 187–202, 233–244. 1915; **16**:1–17, 33–45. 1916.

[18] HAGSTRÖM, J. O., Critical researches on the Potamogetons. Kgl. Svensk. Vetensk. Handl. **55**:no. 5. pp. 281. *figs. 119*. 1916.

features. The stele presents 6 "stages" of development, differing in the number and arrangement of the bundles; while 5 kinds of endodermis are recognized. An interesting series of facts is recorded in reference to the "adaptation of some leaves for a double life," and also their "adaptation for different levels of water." Another adaptation explained is the "arrangements in stems and leaves for the purpose of resisting the impetus of the waves and the current of water," 6 kinds of stem structure being recognized. All of these anatomical variations are not merely observed, but are arranged in evolutionary sequence. Numerous hybrids are recognized by means of the new characters used, as well as by sterile pollen grains and "deformed stigmata." In general, hybrids are very sterile, but sometimes sterility was found to occur also in "genuine species." The 138 species, 37 of which are described as new, and the 62 recognized hybrids are grouped in 26 sections. When it is remembered that *Potamogeton* has been credited heretofore with approximately 65 species, this increase to 200 species and hybrids indicates that it is a much more complex assemblage of forms than has been supposed. In general, the species and hybrids are described in great detail, not only including the ordinary taxonomic characters, but also their anatomy and "biology." In short, the monograph treats of the taxonomy, morphology, anatomy, and ecology of *Potamogeton*.—J. M. C.

Pennsylvania trees.—One of the best of the recent tree manuals issued by various states comes from Pennsylvania.[19] It consists of two parts, the first devoted to an elementary discussion of the principles of forestry, the second consisting of an illustrated manual of the trees of the state. Among the topics treated in an interesting manner are the character of forest stands, their natural and artificial reproduction, the form and structure of trees, including a large number of photographic studies of bark, types and structure of twigs, buds, leaves, flowers, and fruit, and the structure of the wood. In the second part the keys and descriptions appear to be adequate and the illustrations decidedly superior to those usually seen. An entire page is devoted to each species, and the drawings include, in addition to the usual leaves and fruit, careful sketches of the flowers, buds, and leaf scars. The term "tree" is so broadly interpreted as to include such woody plants as *Rhus copallina*, *Acer spicatum*, and *Kalmia latifolia*.—GEO. D. FULLER.

Addisonia.—The fourth number of this finely illustrated journal contains colored plates and popular descriptions of *Sedum diversifolium*, *S. humifusum*, *Catasetum Scurra*, *Chionodoxa Luciliae gigantea*, *Agave subsimplex*, *Dasystephana Porphyrio*, *Cymophyllus Fraseri*, *Rhus hirta dissecta*, *Opuntia vulgaris*, *Tillandsia sublaxa*, and *Echeveria australis*.—J. M. C.

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[19] ILLICK, J. S., Pennsylvania trees. Pa. Dept. Forestry Bull. 11. pp. 232. *pls.* 129. *figs.* 109. 1915.

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A SURVEY OF THE HAWAIIAN LAND FLORA

VAUGHAN MACCAUGHEY

(WITH FIVE FIGURES)

The Hawaiian Archipelago has long been known to the scientific world as a peculiarly isolated island world with many extraordinary biological features. The remoteness of the group from continental areas, the exclusively volcanic nature of the mountains, the extreme specialization of many plant and animal forms—these and many other unique conditions have given particular interest to the biological problems of Hawaii (fig. 1).

It is the purpose of this paper to make a rapid survey of the prominent characteristics and elements of the Hawaiian land flora.[1] The timeliness of such a survey is evident to all who have followed the researches of recent years in the various departments of natural science, as these studies have in many instances necessitated extensive revision of previous records. In order to compress the material within reasonable bounds, much interesting detail is necessarily omitted, and numerous problems of great interest from the standpoint of philosophical biology[2] can here be accorded only passing mention.

[1] For purposes of convenience all of the algae and fungi except the conspicuous woody and fleshy forms are excluded from this consideration of the land flora.

[2] Undoubtedly, after the systematic work on the various groups comprising the Hawaiian fauna and flora has been brought to a stage of comparative completeness, the greatest contributions will be made in the field of philosophical biology. Some of these contributions are suggested in the sections on endemism and precinctiveness in this paper.

For an account of the physical aspects of the Hawaiian Islands, their topography, climate, volcanoes, soils, and geological history, all of which have important and complicated relations with the flora, the reader is referred to such standard treatises as BALDWIN'S *Geography of the Hawaiian Islands*, BRYAN'S *Natural history of Hawaii*, HITCHCOCK'S *Volcanoes of the Hawaiian Islands*, and the excellent article on Hawaii in the latest edition of the *Encyclopedia Britannica*.

FIG. 1.—Map of the larger islands of the Hawaiian Archipelago

Endemism

A few quantitative statements will elucidate the remarkable endemism of the Hawaiian land flora. There are approximately 1200 species of native plants, exclusive of algae, fungi, and bryophytes. This is also exclusive of the 25, more or less, brought in by the primitive Hawaiians, and discussed later in this paper. Of this number about 200 have been introduced and established within historic times, leaving about 1000 genuine indigenous species. Approximately 700 of these are endemic, thus constituting 70 per cent of the vascular land flora. Restricting the

calculation to "flowering" plants alone, it is estimated that *more than 85 per cent* are endemic. This is a proportion unequaled in the annals of geographical botany. It is particularly significant when compared with the 34 per cent of Samoa, 35 per cent of Tahiti, and 53 per cent of Fiji.

New Zealand, with a land area of 100,000 sq. m., 16 times that of Hawaii, has no more species of flowering plants than Hawaii, and its percentage of endemism, about 75, is markedly lower. Japan, with a total area of 175,000 sq. m., some 28 times that of the Hawaiian Archipelago, has but 1500 species of flowering plants, only 300 more than Hawaii. There is no other region on the earth, of similar area, with so large a list of endemic forms as Hawaii.[3]

In addition to the native flora proper, there are probably 1000 additional species in cultivation or semicultivation in the plantations, ranches,[4] gardens, nurseries, and fern and orchid houses of Hawaii. These have been gathered from all parts of the world, with a natural emphasis upon tropical and subtropical species.

The lucid and comprehensive statement of PERKINS, the eminent student of Hawaiian zoology, is pertinent at this point.

> A comparative study of the many groups of animals represented in the islands, and of the affinities of species to species, and genus to genus, in the groups of allied forms, has led me to believe in the extreme rarity of a successful immigration from outside. The extraordinary gaps in the fauna of whole families of wide distribution, and containing countless species, many of which no doubt would, and some of which after introduction by man are known to thrive in the islands, show clearly how hardly and rarely have immigrants reached them from outside. A limited number of birds and insects, species of well known migratory habits, for which no seas are impassable, doubtless arrive continuously, but these, only in the event of such migration ceasing, are likely to produce new and endemic forms.
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> The phenomena exhibited by the flora appear to me to be extremely similar to those of the fauna. There may be seen the same notable absences

[3] See LYDGATE, The endemic character of the Hawaiian flora. Thrum's Hawaiian Annual. 1911 (pp. 53–58).

[4] Extensive areas on Hawaii, Maui, and Molokai, for example, aggregating hundreds of square miles, are overrun with introduced ranch grasses. These form a dense continuous sod, which not only drives out the native grasses and herbs, but also prevents the germination of seeds of the forest trees and other native plants.

of forms widely distributed elsewhere, the same multiplication of allied species of many of the genera that are present, the same groups of allied genera, embracing many species. I believe that the explanation of these facts is quite in accordance with that which I think to be true of the fauna, as above stated. . . . . The present Hawaiian fauna is derived from waifs and strays from all directions. At rare intervals from the Eocene till now chance immigrants have arrived. Some have been able to establish themselves, many more probably, even after a landing had been effected, have failed. Those that have been successful and have found congenial conditions have often thriven amazingly, giving rise to hosts of descendant species, as they have become adapted to or become modified by diverse conditions. . . . . Where conditions have proved favorable and remained so, and plant or animal has become adapted to special conditions, an exuberance of distinct forms has sprung from the ancient immigrant. Such cases are manifest in the Lobeliaceae amongst plants, and in many groups of animals, the Drepanididae (birds), Plagithmysidae (insects), Achatinellidae (mollusca), and many others. Such form the chief and most interesting part of the native fauna and flora of the present day.[5]

Precinctivity

A second notable feature of the flora is the highly precinctive ranges of many species and varieties. This sharply defined localization of habitat has reached a very advanced stage with many forms. The condition is closely analogous to the equally remarkable precinctive distribution of the arboreal snails (Achatinellidae), and many of the native birds and insects, and is undoubtedly due to the same environmental and evolutionary factors.

The statement may be made conservatively that a very large percentage of the endemic Hawaiian plants are closely confined within areas of a few square miles, and in many instances of a few square rods.[6] Thorough botanical explorations of the past few

[5] From PERKINS' introduction to the *Fauna Hawaiiensis*, being the land fauna of the Hawaiian Islands; by various authors; published in 6 parts, 1899–1913. Cambridge University Press. It may be remarked that endemism is strongly exhibited among the Hawaiian lizards, crabs, holothurians, madreporarians, and various marine groups. See also GULICK, JOHN T., Evolution, racial and habitudinal. Carnegie Inst. Washington. 1905, especially pp. 1–5, dealing with endemism of Hawaiian land shells.

[6] MACCAUGHEY, V., Precinctive flora of the Waianae Mountains. Hawaiian Forester **13**: 85–89. 1916; and *Gunnera petaloidea* Gaud. Amer. Jour. Bot. **4**: 33–39. 1917.

years have failed to disclose new habitats or localities for many of these precinctive plants. For example, *Drosera longifolia* occurs only in the summit bogs of Kauai; *Pelea pallida* is limited to Kaala, in the Waianae Range; many of the lobelias, cyrtandras, and kaduas are sharply precinctive; *Lagenophora mauiensis* occurs only in the Eeka swamps; and 40 or 50 other well defined illustrations might be cited.[7]

The limitations of this paper forbid any extensive discussion of the remarkable geological history of the Hawaiian Archipelago, and the bearing of this history upon the development of the land flora.[8] It is sufficient to state that the older islands lie to the westward, and that the eastern end of the chain comprises the youngest elements of the group. Many years ago HILLEBRAND noted the contrast between the vegetation of Kauai and Mauna Loa as two extremes. He stated that "the Kauai species of the leading Hawaiian genera are in all instances the most specialized, to be distinguished by more striking characters than the others. Examples are *Schiedea, Raillardia, Dubautia, Campylotheca, Lipochaeta, Pittosporum*, and *Pelea*. The proportion of species peculiar to Kauai with species peculiar to all the other islands is about 67:382, or 17.5:100."

The studies and explorations of succeeding botanists have tended to confirm and intensify this contrast. Kauai, Waianae on Oahu, the east end of Molokai, West Maui, Kohala and Puu Waa-waa on Hawaii, these are regions much more ancient than the land areas with which they are immediately connected, and their vegetation gives abundant evidence of their antiquity. During the summer of 1916 Professor W. A. BRYAN, of the college of Hawaii, made explorations on the summits of the high mountains of Hawaii which gave abundant and conclusive evidence of a former period of glaciation. His notable discoveries add to the

[7] MACCAUGHEY, V., Vegetation of the Hawaiian summit bogs. Amer. Bot. **22**: 45–52. 1916.

[8] The geological researches of recent years have demonstrated that the islands are by no means simple in structure, as was once believed, but on the contrary show innumerable evidences of prolonged and profound geological changes. The complexity of these changes has only lately been fully appreciated, and their unraveling will require painstaking research for many years to come.

accumulating data which point to the great antiquity of this archipelago and to its complex geological history.

Extinction

The flora of today strikingly illustrates the profound biological changes concomitant with the coming of foreigners[9] and the spread of their industries. Practically all of the arable lowlands have been converted into plantations, and are covered with sugar cane, pineapples, and other crops. The level uplands have become sheep and cattle ranches. Agriculture has wiped out practically all the native vegetation in all of these utilizable regions, and the indigenous flora is now largely confined to the mountains and the waste lands.

Feral and semi-wild goats, sheep, swine, and cattle have been the most serious and persistent foes of the native flora. For over a century they have roamed almost unchecked through the forests, overrunning the mountainous districts, and in some instances whole islands. They have totally destroyed or irreparably damaged untold quantities of indigenous vegetation. Many districts have been stripped of all save the weediest and least edible of plants. Some of the smaller islands (Niihau, Lanai, and Kahoolawe) that have long been overstocked with these herbivorous vandals have been depleted almost wholly of the original native flora. The destruction of the vegetative protective covering has exposed these regions to the full force of erosion by wind and water, and this has resulted in the removal of huge quantities of surface soil.

It is difficult to conceive the transformations wrought in the Hawaiian forests by man[10] and his live stock, so extensive have been the devastations. Many herbaceous species have undoubtedly been totally exterminated. Some of the woody species that have become extinct within historic times, or are now on the verge of

[9] Foreigners, that is, others than native Hawaiians; especially Americans, British, Germans, etc.

[10] In the early days the woodlands in the vicinity of the numerous sugar mills and plantations were cut to supply fuel for the mills, and for the plantation villages. The latter use continues to the present time, and there is a serious shortage of firewood on all the islands.

extinction, are *Neowawraea phyllanthoides, Alectryon macrococcus, Alphitonia excelsa, Hibiscadelphus Giffordianus, H. Wilderianus, H. hualaliensis, Kokia Rockii, K. drynarioides, Clermontia haleakalensis, Cyanea arborea, C. comata,* and *Hesperomannia arborescens.*

It may be estimated conservatively that probably several hundred species of angiosperms have become extinct since the first landing of live stock on these islands. PERKINS has estimated that 300 species of native insects have been exterminated. The extinction of many of the highly specialized avian species is a lamentable and widely known fact. On the island of Oahu, for example, there are more extinct species of endemic birds than existing species. Numerous forms of the arboreal snails are now excessively rare.

Ocean currents

Hawaii is so remote from other land areas, and is so situated with reference to the great trans-Pacific ocean currents, that comparatively few plants have been added to her flora through the agency of water borne seeds. The shores and beaches present a striking contrast to the forested littoral of many South Pacific Islands, which have been well stocked with plants by the currents.[11]

Logs of coniferous species are thrown upon Hawaii's windward shores after a long drift from the northwest coast of America. These have probably brought seeds and spores in their crevices, although there is no conclusive evidence on this point.[12] BRYAN'S hypothesis is very suggestive in this connection. "It is possible that in bygone ages, long ago, the movements of the Pacific may have been reversed, so that various plants from the Australian, Polynesian, and South American regions that are well known here, might have been carried to the islands by them, in one way or another."

Some of the species that very probably have been introduced by ocean currents are *Scaevola Lobelia, Heliotropum curassavicum,*

[11] Seeds of the following woody species are common in the drift material along the beaches: *Aleurites moluccana, Calophyllum Inophyllum, Terminalia Catappa, Mangifera indica, Cocos nucifera, Thespesia populnea, Pandanusodo ratissimus.*

[12] See WARMING, E., Botany of the Faroes. Copenhagen. 1903 (Vol. 2, pp. 660–681; particularly pp. 674–678, on plant immigration across the sea).

H. anomalum, Vitex trifolia, Ipomoea pes-caprae, I. acetosaefolia, I. bona-nox, I. tuberculata, Vigna lutea, Mucuna gigantea, Batis maritima, Sesbania tomentosa, Capparis sandwichiana, Erythrina monosperma, Ruppia maritima, Colubrina asiatica, Dioclea violacea, Strongylodon lucidum, Caesalpinia Bonducella, Cassytha filiformis, and numerous grasses and sedges.

HITCHCOCK cites *Pandanus* as a typical current disseminated plant.

> A good illustration of the origin of the vegetation is the screw pine, *Pandanus*, or lau hala. . . . . These seeds will stand saturation in water for months without losing their vitality. Hence they may be carried hundreds or thousands of miles from the place of their nativity, and when washed inland by unusually high waves will be placed where they will sprout and grow up. I once saw a place in Kauai where hundreds of young lau halas had started to grow near the seashore. . . . . There is no tree with wider range in the Pacific than the *Pandanus*. And it was in existence in the Triassic period in Europe. It is therefore one of the oldest and most persistent of plants, and the one best fitted to start plant life on the isolated volcanic islands for the first time peering above the waves.[13]

Duration of migration

The philosophical presentation of the status of Hawaiian plant immigrants with reference to the evolution of endemic forms has been made so comprehensively by PERKINS that an extract from his statement is given here.

> Although endemicity of plant or insect, as represented by great peculiarity of structure and usually by the occurrence of numbers of allied species, naturally indicates a very ancient occupation of the land by their immigrant ancestors, yet it does not necessarily follow that paucity of species or the apodemicity of a genus denotes a comparatively recent immigration. A classification of the flora, as belonging to a definite age or era, based on such a supposition will certainly prove erroneous. It is not probable that all immigrants that arrive and become established are able, even after vast time, to become adapted to such diverse conditions as others, and some doubtless are much more slow to do so than others.
>
> The evolution of new genera or species would proceed in a very different manner in different cases. In judging the length of time that any particular

[13] It is quite possible that the *Pandanus* was first brought to the islands by the ancient Hawaiians, from their home in the South Pacific, where this tree is abundant; see concluding section of this paper. Also see GATES, F. C., The pioneer vegetation of Taal Volcano. Philippine Jour. Sci. 9:391–434. *pls. 8.* 1914.

plant or group of allied plants has existed in the islands, the botanist would be well advised to consider the fauna that is especially attached to these. When one considers that trees little modified from foreign species, for example, *Acacia koa* or *Sophora chrysophylla*, possess a great endemic fauna, not only species, but even genera of birds and insects, quite restricted to or dependent on them, and that some of these creatures are certainly themselves not less remarkable in their peculiarities than the most peculiar of the composites or lobelias, we may hesitate to attribute such plants to a later era than many other elements of the flora, which at first sight appear far more ancient.

Again, while in the islands an abundant endemic fauna restricted to a plant indicates an ancient occupation by the latter, the absence of such a fauna does not necessarily imply the reverse. In a fauna of comparatively few types it may happen that few or no species have reached the islands that could become adapted to certain elements even after great length of time. I think that those who are in favor of the comparatively frequent accession of immigrants to account for the great series of allied species, or groups of allied genera, hardly make full allowance for the great age of the islands. HITCHCOCK remarks in writing of the most recent portion of the group, the still active Mauna Loa on Hawaii, when one considers how little the bulk of the mountain is made up of the few flows delineated on the map, and how small a portion of the whole mass these can be, he is overwhelmed by the certainty that there were millions of streams and that millions of years must be assumed in order to say how old the mountain is. It must have commenced to build up long before the Tertiary period. And here he is considering the most recent portion of the group, and not the vastly more ancient parts.[14]

It is significant that the gymnosperms are entirely absent from the native Hawaiian flora; cycads and conifers have been introduced in recent years.

Zonation

In the Hawaiian Archipelago the large ecological zones are well defined. Elevation above sea level and precipitation are the two dominant factors which determine the local phytogeography. The zonal distribution of the endemic and indigenous vegetation is very pronounced; a very general statement may be made to the effect that the flora perceptibly changes in kinds and quantities of species with every 1000 feet of ascent (figs. 2–5). The following synopsis of the chief zones will serve to indicate the important phytogeographic areas:

[14] See also SCHIMPER, A. F. W., Die Indo-Malayische Strandflora. Jena. 1891.

1. Littoral.—(*a*) *Humid littoral*, along the windward coasts; (*b*) *arid* or *semiarid*, along leeward coasts and coasts far removed from the mountainous interior.

2. Lowlands.—Up to 1000–1500 ft., with humid and arid sections, depending upon relation of topography to trade winds and distance from interior mountains.

3. Forest zone.—(*a*) *Lower forest* (1000–2000 ft.), with humid and arid sections; in early times this zone extended much farther seaward on the various islands than it does now; (*b*) *middle forest* (1800–5000 ft.), range variable, with humid and arid sections; this comprises in the humid areas the typical Hawaiian rain forest, highly hygrophytic and very rich in endemic forms; (*c*) *upper forest* (5000–9000 ft.), restricted to the high mountains of Maui and Hawaii.

FIG. 2.—View from a dividing ridge between 2 long humid valleys, looking toward the head of Kau-kona-hua Valley; fog-covered summit ridge, elevation 2500 ft., seen in distance; entire region covered with dense and unbroken rain forest; on slopes and ridges trees average 15–30 ft. in height, in valley and ravines they rise to 40–60 ft.; annual precipitation at head of this valley approximates 200–300 inches.

4. Summit regions.—(*a*) *Xerophytic summits* (9000–14,000 ft.); high mountains of Maui and Hawaii; (*b*) *hygrophytic summits* (4000–6000 ft.); peaks rising into the cloud zone, with summit bogs.

Palms

The palms furnish an interesting illustration of the 3 floral elements: indigenous, native introductions, and modern introductions.[15] The capital city, Honolulu, is a veritable palm garden; there are some 80 species represented, which have been gathered from all parts of the tropics. There is scarcely a home or yard without its palms; some of the finest driveways are colonnaded with such stately species as *Oreodoxa regia* and *Phoenix dactylifera;*

FIG. 3.—Arid, deeply eroded summit ridge, elevation 2000 ft., of eastern Koolau Mountains; absence of vegetation due partly to aridity, partly to devastations of goats; remnants of original forest cover occur here and there in hanging valleys near sky line and in deep ravines.

and certain of the old estates, the famous Hillebrand gardens for example, are crowded with rare and choice specimens. The only palm introduced by the natives (and this introduction is necessarily more or less theoretical, in the absence of historical records) was the coco palm. This species (*Cocos nucifera*) is widely spread throughout Polynesia, and in early times formed a characteristic feature of many Hawaiian shores and beaches.

[15] MACCAUGHEY, V., The economic woods of Hawaii. Forest Quarterly 14: 696–716. 1916.

The indigenous palms are confined to the single genus *Pritchardia*, and are all endemic. There are a number of Hawaiian species, perhaps a dozen. The exact botanical status of these has not as yet been fully determined. The species of *Pritchardia* occur mainly in the rain forests and along exposed humid summit ridges. They are scattered, are usually solitary or in small clumps, never form pure stands, and constitute a very minor element in the forest. From the standpoint of abundance or striking features,

FIG. 4.—Xerophytic promontory, Ka-ena Point, a typical "dry ridge" formation; other similar ridges, separating arid valleys, seen to the right; in foreground a coral beach formation covering ancient lava beds; note stratification of lava flows in the faces of promontory, also extensive talus slopes.

the native palms are as disappointing as the native orchids. They occasionally attain considerable height (40–50 ft.), but are customarily of short or even dwarf stature. *Pritchardia* is confined to the islands of the Pacific. The Hawaiian species show close affinities with those of the South Seas.

Many of the other monocotyledonous families are but meagerly represented. The Orchidaceae, for example, that attain unrivaled

luxuriance and marvelous specialization in many tropical regions, have only 3 species in Hawaii, and these are all shy, poor, homely little plants.[16] *Pandanus* is represented by one species, formerly abundant in the lowlands. *Freycinetia Arnotti* Gaud. is a tall woody liana, common in the lower forest zone of all the islands, and often forming dense jungles.

The liliaceous plants of Hawaii are in part woody species; none are bulbs, and none have particularly showy flowers. Of the

FIG. 5.—Lava flow of the smooth or "pa-hoe-hoe" type; shows invasion by lichens and ferns; in arid situations lava flows retain a new, fresh appearance for a long period of years; under humid conditions they rapidly disintegrate and are soon covered with plant life.

5 genera, 3 are monotypic: *Cordyline terminalis*, a tall shrub; *Dracaena aurea*, a tree; and *Dianella odorata*, a large herbaceous perennial; all are abundant. *Astelia* and *Smilax* are confined to the forest and upper zones, and none of the group occur on the coastal plains or lowlands. There are no "fields of lilies" in Hawaii. *Commelina nudiflora* is exceedingly abundant in moist

[16] MACCAUGHEY, V., The orchids of Hawaii. Plant World 19:350–355. 1916.

situations throughout the lowlands, forming pure stands and smothering other vegetation.

The large and highly diversified tropical order of the aroids has no place in the Hawaiian flora, except 2 naturalized species, *Colocasia* and *Alocasia*, introduced by the ancient Hawaiians. *Colocasia antiquorum*, the kalo or taro, was the staple food of the primitive Hawaiians. The plant was raised both in irrigated fields (*loi*) and on the uplands (*Kula*). *Alocasia macrorrhiza*, the ape or giant taro, was raised in clearings in the lower forest, and used chiefly in time of famine. Ornamental aroids of many genera are now abundant in Honolulu gardens, but these are strictly exotic, and none of these are naturalized.

Another group that one naturally associates with a tropical background is the Begoniaceae, and yet of the 400 species, only one is native to the Hawaiian Archipelago. Our lone species is endemic, and is so distinct from its relatives that it has been placed in a monotypic genus, *Hillebrandia*. It is a beautiful plant with ornamental foliage and fine showy clusters of pink flowers, but is limited to such isolated and difficult regions that few people, either natives or whites, have seen it.

Lobelias

Unquestionably the crowning glory of our flora are the arborescent lobelias. These constitute one of the unique elements of the Hawaiian forest flora, and aggregate some 100 species, distributed among 6 genera, 5 of which are endemic. As ROCK[17] succinctly states, "nowhere in the world does this tribe reach such a wonderful development in such a comparatively small area."

The lobelias surpass in number of species all other plant families comprising the Hawaiian land flora. Many of the species show extreme specialization. The extraordinary range of variation strongly suggests that we are witnessing the last spasmodic outbursts of the evolutionary impetus of this group. Quite unlike the small herbaceous lobelias familiar on the continent, all of our species have stout woody stems. The majority are tall shrubs or

[17] ROCK, J. F., Synopsis of the Hawaiian flora. Thrum's Annual, Honolulu. 1912 (pp. 82–91).

trees, and some reach the amazing height of 40 ft. Many species have a slender, naked, palmlike trunk, closely marked with conspicuous leaf scars. This pole terminates in a large rosette of foliage and a showy inflorescence. These and other characters give the plant a deceptively primitive aspect.

The Hawaiian genera are *Brighamia*, endemic, 1 species; *Lobelia*, 5 endemic species; *Clermontia*, endemic, 17 species; *Rollandia*, endemic, 6 species; *Delissea*, endemic, 7 species; *Cyanea*, endemic, about 45 species. There are many features, both structural and ecological, which strongly suggest that our lobelias are the remnants of a very ancient flora, a flora that has well nigh been obliterated by profound geological and climatic changes.

It is significant to observe that the other islands of the Pacific are practically lacking in lobelias. Furthermore, in other parts of the world these plants are notably alpine in distribution. Many high mountains of the tropics and subtropics are marked by a lobeliaceous flora similar to that of our Hawaiian mountains. These and other facts in local phytogeography lean strongly toward the geological hypothesis that at one time these island mountains stood at a much higher level (perhaps thousands of feet higher) above the sea than at present. Under this theory the islands as they now stand are but the vestiges of a former extensive land mass.[18] PILSBURY uses this hypothesis to explain the extraordinary geographic distribution of the Hawaiian arboreal mollusks. It undoubtedly has an application to such phytogeographic problems as are involved in any attempt to elucidate the origin of the Hawaiian lobelias.

Cyrtandras

One of the largest of the Hawaiian genera, and notably rich in endemic species and varieties, is *Cyrtandra*. The genus ranges throughout the islands of the Indian and Pacific oceans and in China, with a total of about 200 species. Of the 30 or more Hawaiian species, all are soft-wooded shrubs, and practically all are endemic. The remarkable variability of the genus is manifest

[18] HILLEBRAND, WILLIAM, Flora of the Hawaiian Islands. 1888; published posthumously; out of print for many years; the standard flora of the islands, although now in serious need of taxonomic revision.

to a high degree by many of our species. As HILLEBRAND states, "the polymorphism of the Hawaiian cyrtandras is extraordinary; no single form extends over the whole group, and not many are common to more than one island. The variations affect every part of the plant, and branch out and intercross each other in manifold ways to such an extent that it is next to impossible to define exact limits of species."[19] The evolutionary status of our species is closely analogous to that of the native lobelias.

The species of *Cyrtandra* are largely confined to the humid regions; they are precinctive and extremely shade-tolerant. Many species are to be found only in the narrow-walled ravines and dimly lighted recesses of the rain forest. *C. cordifolia* Gaud., *C. Pickeringii* Gray, *C. gracilis* Hbd., *C. Kahilii* Wawra, *C. grandiflora* Gaud., *C. paludosa* Gaud., *C. latebrosa* Hbd., and *C. Lessoniana* Gaud. are representative Hawaiian species of this genus.

Composites

Second only to the lobelias in importance are the Compositae. There are over 80 species, representing 29 genera; of these, 60 species are distributed among 9 endemic genera. Several of the genera (*Argyroxiphium*, *Wilkesia*, *Hesperomannia*, and *Remya*) show many evidences of isolated and specialized evolution and, as HILLEBRAND remarks, "probably belong to the oldest denizens of our islands, a supposition countenanced by the fact that each holds no more than two species." With reference to the last statement it must be remarked that several new forms in these groups, probably of specific rank, have recently been discovered.

A number of these peculiar Compositae (*Artemisia*, *Dubautia*, *Raillardia*) are arborescent, and alpine in habitat. On the high mountains of Maui and Hawaii they reach an elevation of 10,000 feet. *Lagenophora* is a peculiar summit bog form.

To this family belongs one of the most famous of Hawaiian plants, the beautiful silver sword (*Argyroxiphium sandwicense*). This plant has a large, compact basal head of dagger-shaped leaves

[19] WINNE, W. K., Intercontinental land connections and their relations to plant migrations. Chicago. 1914 (p. 24, "The Pacific continent").

densely covered with shining silvery pubescence; from this body arises a tall inflorescence (6–8 ft.) of showy purple flowers. This unique herbaceous perennial is xerophytic, and occurs only at high elevations on Maui and Hawaii.

Lipochaeta, *Coreopsis*, and *Tetramolopium* are large genera of herbaceous or semiligneous perennials; there are 10 or 12 species in each genus, mostly endemic. The flowers are small, but very numerous, and form showy masses of rich yellow. *Bidens*, *Ageratum*, *Xanthium*, *Sonchus*, *Vernonia*, *Erigeron*, *Gnaphalium*, *Franseria*, *Eclipta*, and *Centaurea* are common weeds of the roadsides and fields.

Modern research in ornithology has demonstrated the existence of several bird migration routes from South America to the north via Hawaii. The Hawaiian goose and the Pacific golden plover furnish specific instances of these long over-sea migrations. Inasmuch as a number of the endemic composites show close affinity with certain Andean and other South American species, it is highly probable that they were carried thither by migrating birds.[20]

A number of other native plants were probably brought by the same agencies, for example, *Rubus*, several endemic species, closely related to Pacific Coast forms; *Nertera depressa*, with fleshy red drupes, a South Pacific Coast species; *Fragaria chilensis*, which also occurs along Pacific America; *Dodonea viscosa*, with glutinous capsules, and widely dispersed; *Lycium sandwicense*, and others.

Leguminosae

The vast family Leguminosae, rivaled in size and distribution only by the Compositae, is abundantly represented in our flora. There are nearly 30 genera, many of comparatively recent introduction, but now well and widely established. Four genera, *Acacia*, *Sophora*, *Mezoneurum*, and *Erythrina*, are arborescent. Endemic species occur in *Vicia*, *Canavalia*, *Vigna*, *Acacia*, *Mezoneurum*, and *Sophora*. There are many introduced leguminous plants in Honolulu; particularly conspicuous are the flowering

[20] See ERNST, A., The new flora of the volcanic Island of Krakatau. Trans. by SEWARD. Cambridge. 1908 (pp. 58–60, "Seed-dispersal by birds").

trees of *Cassia*, *Poinciana*, *Peltophorum*, *Pithecolobium*, and allied genera.[21]

A number of the indigenous legumes are beautiful, high-climbing woodland vines, with showy clusters of bright colored flowers; *Syrongylodon lucidum*, *Vicia Menziesii*, *Mucuna urens*, *Dioclea violacea*, and *Canavalia galeata* are examples of these. Species of *Crotalaria*, *Indigofera*, *Leucaena*, *Acacia*, *Mimosa*, *Dolichos*, *Medicago*, *Phaseolus*, and *Desmodium* are common roadside weeds. The most valuable and widely known of our cabinet woods, *koa*, is from the common forest tree *Acacia koa*.

Rubiaceae

The Rubiaceae comprise a large and diversified portion of our flora. There are 13 genera, of which 4 (*Kadua*, *Gouldia*, *Bobea*, and *Straussia*) are endemic. There are between 50 and 60 rubiaceous species; of these the majority are tall shrubs or arborescent. The other genera (*Gardenia*, *Plectronia*, *Coffea*, *Morinda*, *Psychotria*, *Paederia*, *Nertera*, *Coprosma*, and *Richardsonia*) occur in many other tropical regions.

Of special interest, because of their beautiful flowers, are the two endemic species of *Gardenia*. The blossoms are large, white, deliciously fragrant, and rank high among the wild flowers of Hawaii. The coffee (*C. arabica*) was introduced in 1823, and its cultivation spread rapidly to all of the larger islands of the group. Although a combination of economic and cultural factors has largely suppressed the coffee industry, the plant itself is thoroughly naturalized, and occurs in many of the humid lower regions. Birds have undoubtedly assisted in its dissemination.

Rutaceae

Rutaceous trees and shrubs comprise a conspicuous and abundant element in the native forests. There are few groves or wooded slopes that do not contain a generous proportion of rutaceous

[21] The algaroba or mesquite (*Prosopis juliflora*) was introduced nearly a century ago, and has become widely spread through the agency of cattle. Today it is one of Hawaii's most valuable trees, and is abundant on the lowlands to the 2000 foot contour. It is an important source of honey, nutritious pods, and firewood, and greatly ameliorates the soil upon which it grows.

species. Two of the three genera (*Pelea* and *Platydesma*) are endemic; the third (*Zanthoxylum*) is world wide in its range. *Pelea*, named in honor of the Hawaiian volcano goddess Pele, is a large genus, with nearly 30 recognized species and an even larger number of varieties. Like the species of *Cyrtandra* and the lobeliaceous genera, the species of *Pelea* are highly variable, with many intergrading forms, so that as yet the species are poorly defined.

Platydesma is an isolated genus, with 4 woody species. *Zanthoxylum* has 7 species, 6 arborescent, and many varieties. The majority of these are characteristic of arid leeward regions and old lava flows. There are no native citrus fruits, although the orange has become naturalized in many districts, particularly in the Kona district, on Hawaii.

Violaceae

The endemic Violaceae are a distinct surprise to the mainland botanist on his first excursions in our Hawaiian forests. Instead of tender little herbs, he finds stout woody shrubs, ranging in height from 3 to 6 ft. The flowers are quite like those of the familiar eastern violets, and are white, pink, purple, or blue in color, according to species. There are 7 or 8 species, ranging in habitat from hot, exposed, semiarid regions to the cold, rain-soaked summit bogs. They occur on all the islands, and in certain favorable localities, as the Molekai swamps, they cover considerable areas.

Several species, for example *V. helioscopa*, have large showy flowers of great beauty and fragrance, and suggest novel horticultural possibilities in the way of cultivated violet bushes. Undoubtedly, as familiarity with the native flora increases and methods for transplanting and culture are improved, some of these lovely shrubs will be utilized in horticulture.

Araliaceae

This large and widely distributed family is prominent in the Hawaiian flora. All of our species are trees, and many of them form a conspicuous feature of the xerophytic woodlands, inhabiting the barren lava fields and other arid regions. The Araliaceae had two great centers of distribution, tropical America and Malaya.

It is probable that Hawaii originally received its contribution from the Malayan center, although its 4 genera are now almost wholly endemic.

All of the 13 or more Hawaiian species are endemic, and of these a number are sharply localized in their range. The 4 genera are represented as follows: *Tetraplasandra*, 7 spp.; *Reynoldsia*, 1 sp.; *Pterotropia*, 3 spp.; *Cheirodendron*, 2 spp. The characteristic American-Asiatic genera *Aralia* and *Panax* do not occur in Hawaii.

Labiatae

The Labiatae are represented by 7 genera. Three (*Stenogyne* with 16 to 18 species, *Phyllostegia* with about 20 species, and *Haplostachys* with 3 species) are endemic. *Plectranthus* comes from Australia, and *Sphacele* from the Pacific Coast of America. The two remaining genera (*Salvia* and *Stachys*) are weeds of world-wide geographic range.

Hawaii has no equivalent for the familiar mints of eastern fields and waysides, such as catnip, peppermint, pennyroyal, hoarhound, and a score of others. Our *Sphacele hastata*, endemic from an Andean genus, is a typical example of precinctiveness. It forms an extensive belt around the great volcanic mountain Hale-a-ka-la at an elevation of about 3000 ft., and occurs nowhere else in the archipelago.

Many of the shrubby species of *Phyllostegia* and *Stenogyne* have lovely masses of flowers, white, pink, and red, and give beautiful color effects against the dark greens of the rain forest and the wet shadowy jungles which they inhabit.[22]

Malvaceae

The Malvaceae constitute a large family, dispersed over the whole world, except the arctic regions, and richly represented in the tropics and subtropics. Hawaii is well endowed with this group. There are 2 endemic genera: *Kokia*, the Hawaiian tree cotton, with 2 species; and *Hibiscadelphus*, with 3 species. All of these are excessively rare and localized.

[22] MACCAUGHEY, V., The wild flowers of Hawaii. Amer. Bot. **22**:97–105, 131–135. 1916.

The large genus *Hibiscus* has 6 or 7 native species, all shrubs or trees, with large flowers of striking beauty. The blossoms are white, pink, red, or yellow, according to species, and form a distinctive feature of the rain forest.

The cosmopolitan genera *Malva*, *Malvastrum*, *Sida*, and *Abutilon* are common on the semiarid lowlands. *Gossypium*, the true cotton, includes the unique Hawaiian cotton, *G. tomenlosum*, a spreading shrub, endemic, densely covered with white tomentum, and growing in arid situations along the coasts.

Solanaceae

Of the 70 genera of this family, only 3 (*Solanum*, *Nothocestrum*, and *Lycium*) comprise elements in our native flora. There are many introduced Solanaceae (*Physalis*, *Datura*, *Nicotiana*, etc.), some brought in at a very early period and now thoroughly established. The genus *Solanum* has 6 endemic species, one arborescent; in addition to these there are a number of weeds belonging to this genus. *Nothocestrum* is an endemic genus of 4 arborescent species, and is closely related to the Brazilian genus *Athenaea*. *Lycium*, a genus of 70 species, is represented in our flora by a single widely distributed littoral species.

Grasses

The grasses, including many introduced and now naturalized species, have about 40 genera in the flora. None of these are endemic, although there are a number of endemic species. Some of the more important genera, from the standpoint of distribution and number of species, are *Bromus*, *Calamagrostis*, *Cenchrus*, *Chloris*, *Chrysopogon*, *Cynodon*, *Dactylis*, *Eleusine*, *Eragrostis*, *Festuca*, *Heteropogon*, *Holcus*, *Koeleria*, *Lolium*, *Panicum*, *Paspalum*, *Poa*, and *Stenotaphrum*.

The highly developed sugar-cane industry has monopolized most of the arable lowlands, and needs no further comment here. Rice and corn are also raised; in early times wheat, barley, and oats were exported to California, but are now imported. Clumps of *Bambusa vulgaris*, early naturalized, are scattered here and there in the humid valleys. The prevalent lawn grass in Hawaii is the Bermuda grass, *Cynodon dactylon*.

The representation of Cyperaceae is roughly as follows: *Cyperus* 17 spp., *Kyllingia* 1, *Fimbristylis* 4, *Eleocharis* 1, *Scirpus* 2, *Hypolytrum* 1, *Rhynchospora* 4, *Cladium* 1, *Baumea* 1, *Vincentia* 1, *Gahnia* 5, *Oreobolus* 1, *Scleria* 1, *Uncinia* 1, *Carex* 5.

Absent pests

Hawaii is entirely free from any plants poisonous to the touch. To the botanist familiar with the distressing prevalence of these pernicious vines and shrubs in the continental woodlands, it is a relief to work one's way through a Hawaiian jungle with the certainty of complete safety in this regard. Neither are there any stinging nettles. *Mucuna urens*, the well known "cow-itch" plant, whose pods are covered with stinging hairs, is naturalized in certain restricted areas on the islands of Maui and Hawaii.

The Anacardiaceae are represented in Hawaii by a single arborescent Asiatic *Rhus* (*R. semialata* Murray var. *sandwicensis* Engler). This species extends from India and the Orient to Hawaii, and is non-poisonous. Our variety is a small tree, growing in isolated clumps in all the islands.

It is to be hoped that the pernicious *T. vernix*, *T. radicans*, and *T. Toxicodendron* of North America may never by any accident reach Hawaii. The noisome *Paederia foetida* was accidentally introduced a number of years ago, and its seeds, like those of *Rhus Toxicodendron*, are abundantly distributed by birds. It is now a pest in many of the valleys, as it smothers all other vegetation.

Ferns

There are 43 genera and 185 species of pteridophytes; of these, 2 genera and 118 species are endemic. There are 18 genera with all or 75 per cent and over of endemic species; 18 genera possess no endemic species, or have 75 per cent or over of non-endemic species; 33 species are practically cosmopolitan; 8 species have the west coast of America as their chief station; 22 species have the South Pacific as their chief station; and 2 species have the east coast of Asia as their homeland.

The fern flora of Hawaii is rich and diversified. Like the lichens and the mosses, the ferns are to be found in all habitats,

from the arid raw lava flows to the most humid portions of the jungle forest. A number of species (*Cibotium* and *Sadleria*) attain arborescent stature (8–35 ft.) and many others are of large size.[23] The other extreme is found in the minute Hymenophyllaceae. These are abundant in the rain forest, and clothe the trees with their filmy fronds.

There are about 22 genera of true ferns. The largest of these are *Asplenium*, 40 spp.; *Dryopteris*, 21; *Polypodium* 14, *Elaphoglossum* 8, *Diellia* and *Athyrium* 6, *Sadleria* 5, *Trichomanes* 4. The number of species in the larger genera, and in some of the smaller as well, must be stated as approximations, as many of these species are in serious need of revision. Many of the forms hitherto described as varieties will undoubtedly be raised to specific rank upon careful investigation, and numerous specific descriptions require redefinition.

Some of the abundant forms not indicated by the generic list are *Marattia Douglasii*, *Gleichenia* spp., *Gymnogramme javanica*, *Vittaria elongata*, *Nephrolepis exaltata*, *Cystopteris Douglasii*, *Doodya media*, *Odontoloma repens*, *Micropelia* spp., *Schizostegia Lydgatei*, *Pellaea ternifolia*, and *Adiantum* spp. These are all of genera represented by only a few species.

Salviniaceae are represented by a recently introduced *Azolla;* Marsileaceae by 2 endemic species of *Marsilea;* Equisetales are not represented. The Lycopodiales have 3 genera in the flora: *Lycopodium* with 10 spp. and 5 endemic; *Psilotum* with 20 widely distributed species; and *Selaginella* with 3 endemic and 1 other species. About 50 of the Hawaiian pteridophytes are epidendrous; 15 are xerophytic; and about 15 are lithophilous. The great majority inhabit the rain forests at elevations of 1000–6000 ft.

Bryophytes

Mosses are also very abundant, both in dry and humid regions. In the rain forest are many epiphytic species that clothe the trunks and branches with a dense, soggy envelope of greenery. These jungle moss forests are very beautiful. The summit bogs are the

[23] MACCAUGHEY, V., The tree ferns of Hawaii. Amer. Bot. 22:1–9. 1916.

habitats of many mosses, which completely cover the water-saturated ground of large areas, and mask the treacherous quagmire.[24] The liverworts, including the Marchantiales, Anthocerotales, and Jungermanniales, are abundant in the humid regions, many species being epiphytic and epiphyllous. Species of *Marchantia*, *Anthoceros*, and related genera are conspicuous along streamways and in other moist places.

Fungi

The larger fungi are conspicuously absent from the woodlands. There are a few woody brackets, a few dull-colored mushrooms, a few puffballs and trembling fungi. The sum total of all these is insignificant, however, when compared with the rich fungus flora of such a region as the eastern United States. One may gather more fleshy fungi in a day's collecting in New York, for example, than he would find in diligently scouring our forests for a week. This condition is somewhat surprising, as the cool, humid rain forest zone, with its abundance of decaying vegetation, would appear to be favorable for the development of the fleshy fungi. A number of species of slime molds occur in the ravines and jungles. It is to be regretted that no comprehensive study of the Hawaiian fungi has been made.[25]

Lichens are abundant in all parts of the islands. They comprise the first invaders of the freshly cooled lava flows. They luxuriate in the cool humidity of the rain forest and the summit bogs. They cover the exposed cliffs and ledges of the middle zones, and withstand the aridity of the leeward lowlands and of the high mountains (6000–14,000 ft.). The lichen flora not only occupies a wide variety of ecological areas, but furthermore is of considerable richness. No comprehensive statement can be made as to genera and species, as the Hawaiian lichens have never received exhaustive study.

[24] GATES, F. C., A sphagnum bog in the tropics. Jour. Ecology 3; 24–30. *pl. 1. fig. 1.* 1915.

[25] RICHARDS, H. W., Beiträge zur Flora der Hawaiischen Inseln. Vienna. 1878.

BERKELEY, M. J., Description of fungi collected by R. B. HINDS in islands of Pacific. Hook. Jour. 1842.

———, Fungi of the Challenger Expedition. Linn. Jour. 1878.

Aboriginal introductions

Any outline of the Hawaiian flora would be seriously defective that did not give prominence to the numerous plant introductions by the primitive Hawaiians in their migrations from Samoa and the South Seas. Carefully gathered historical evidence has established the fact that during a long period of time, probably several centuries, the ancient Hawaiians maintained intercourse with their kinfolk in the South Pacific, making the long voyages in their splendid canoes. During this eventful period of migration and intercourse with the south, about 25 species of useful plants were consciously introduced by the natives, and perhaps a much larger number unconsciously brought in as seeds and spores. The list includes:[26]

*Colocasia esculenta; the taro; starchy corms used for food.
Ipomoea Batatas; sweet potato; many native varieties.
*Musa sapientum banana; many native varieties.
Artocarpus incisa; breadfruit tree; seedless.
*Cocos nucifera; cocoanut palm; formerly very common.
*Dioscorea sativa; yam; starchy tubers; climbing vine.
*Dioscorea pentaphylla; yam; starchy tubers; climbing vine.
*Alocasia macrorrhiza; giant taro; starchy corms.
*Tacca pinnatifida; arrowroot; starchy rhizomes.
*Jambosa malaccensis; mountain apple tree; delicious fruits.
Saccharum officinarum; sugar cane; several native varieties.
*Cordyline terminalis; ti bush, with sweet, edible roots.
*Piper methysticum; awa vine; famous Polynesian intoxicant.
*Zingiber Zerumbet; wild ginger; common in lower forest.
*Curcuma longa; well known dye plant; yellow rhizomes.
*Aleurites moluccana; kukui or candlenut tree; illuminating oil.
*Calophyllum Inophyllum; kamani tree; shade, wood, and oil.
*Hibiscus tilaceus; hau tree; fiber, wood, and shade.
*Pandanus odoratissimus; hala tree; fiber and food.
*Broussonettia papyrifera; wauke bush; cloth plant of Polynesia.
*Boehmeria stipularis; opuhi bush; fiber plant.
*Thespesia populnea; milo tree; shade and wood.
*Cordia subcordata; kou tree; shade and wood.
Cucurbita maxima; large gourd, for calabashes.
Lagenaria vulgaris; small gourd, for calabashes.

[26] MACCAUGHEY, V., The food plants of the ancient Hawaiians. Sci. Monthly 4:75–80. 1917.

The starred names indicate species that have escaped from cultivation. Many of these have become so thoroughly naturalized and established in the lower forests, on the lowlands, and along the beaches that they are easily confused with the true indigenous flora.

The successful importation of this diversified series of edible, fiber-producing, oil-producing, and other useful plants, from lands so remote, and by methods so primitive, betokens native horticultural skill of no mean importance. As stated by LYDGATE, "the successful introduction, perhaps acclimatization even, must have meant repeated voyages, extending over generations or even centuries. And not time alone, but patience and skill must have been required for the successful introduction of a seedless tree like the breadfruit. Under favorable conditions it is not easy to propagate; exposed to the trying vicissitudes of a long canoe voyage, weeks of wind and weather and open sea, lack of water, burning sun and blighting spray, huddled into the bottom of the shallow canoe, how many, many failures there must have been."

In conclusion, it may be pertinent to suggest that there is an unwritten chapter in the history of Hawaii's introduced flora, namely the introductions possibly made by the early Spanish explorers. They undoubtedly visited the islands repeatedly, long before the discovery by COOK[27]; there are numerous evidences of their intercourse with the natives, and it is not all beyond the realm of probability that some of the plants now thoroughly naturalized were brought in by these early Spaniards.

COLLEGE OF HAWAII
HONOLULU

[27] Historical evidence shows that probably the first Europeans to land on the Hawaiian Islands were shipwrecked Spaniards, in November, 1527. In 1555 they were discovered by the Spanish navigator JUAN GAETANO, over 200 years before the famous discovery by Captain JAMES COOK (1778).

THE GAMETOPHYTES OF TAXUS CANADENSIS MARSH

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 234

A. W. DUPLER

(WITH PLATES XI–XIV)

Introduction

While the European *Taxus baccata* L. has been studied by a number of workers and its morphology is quite well known, up to the present time no accounts have been published dealing in any connected way with the morphology of the American form, *Taxus canadensis* Marsh., records having been made of only a few scattered observations. Although by some, including PILGER (7) in ENGLER'S *Das Pflanzenreich*, *T. canadensis* is considered as merely a subspecies of *T. baccata*, it has seemed worth while to investigate its morphology and compare it with other forms, and especially with the results obtained in the study of *T. baccata*, most of the work in which was done a number of years ago. The present paper gives an account of the male and female gametophytes in connection with other closely related features. Papers dealing with other phases of the morphology will follow.

Material

The material used in this study was collected during the autumn of 1913 and the years 1914 and 1915 at Huntingdon, Pennsylvania, Sawyer, Michigan, and Mount Carroll, Illinois. Chrome-acetic acid was the chief killing agent used, although some material was killed in formalin-alcohol, but on the whole with results less satisfactory than with the chrome-acetic acid. Heidenhain's iron-alum-hematoxylin, safranin with gentian violet, safranin with light green, and sometimes light green as a contrast stain with the iron-alum-hematoxylin were the stains used. The first of these gave the most satisfactory results in most cases, and for most structures.

Historical

Taxus baccata has long been a favorite form for study, the ovule and the seed first attracting attention, and the early work, therefore, relating almost exclusively to these features. The first study of any importance relating to the gametophytes was that of HOFMEISTER (1), who reported some of the more obvious features of both the male and female gametophytes. The history of the male gametophyte has become further known through the work of BELAJEFF (3), STRASBURGER (4), and JÄGER (6). Miss ROBERTSON (18) made some observations, but, in her own words, her "results on the whole simply confirmed previous work." COKER (9) studied the microspores in *T. baccata* and several of its varieties. STRASBURGER'S early work had to do more especially with the ovulate shoot and the ovule, but in 1879 (2) he described the origin of the megaspore mother cells from the hypodermal layer of the nucellus and gave a few observations on the development of the female gametophyte. The best accounts of the female gametophyte are by JÄGER (6), who gave a rather complete description from the megaspore to the mature endosperm, and by STRASBURGER (12), who gave attention particularly to the early stages, especially to the formation of the megaspores and the free nuclear situation. COKER (9) also studied the megaspores.

In *T. canadensis* itself very little work has been reported. HOFMEISTER (1) has a note concerning the proembryo; CHAMBERLAIN (5) studied the condition of the microsporangium at the beginning of October; COKER (9) reports "more than one embryo sac . . . . not uncommon in *Taxus canadensis*"; and THOMSON (15) has studied the condition of the megaspore membrane.

Male gametophyte

MICROSPORES.—CHAMBERLAIN (5) in material of *T. canadensis* Marsh. collected in the Chicago region, October 1, 1897, found the microsporangium in the spore mother cell stage, and this has been reported (20) as the winter condition. Material collected by the writer, October 10, 1913, shows microspore formation, and material collected at later dates from several localities and in different years in all cases shows the microspores already formed. The

sporangium develops during the summer, and by the time mentioned the microspores are forming (figs. 2–12). In a single strobilus all stages from spore mother cells to completed tetrads may be found. Different stages are also found in a single sporangium, although here the range is not so great as in case of the entire strobilus.

Reduction in the chromosome number and the formation of microspores take place as the result of the usual two divisions of the mother cell. The first division (figs. 2–5) results in two hemispherical cells, and this is followed by the second division (figs. 6, 7), usually in the same plane, resulting in the bilateral tetrad of microspores, although the two planes of division may sometimes be at right angles to one another. Sometimes the second divisions are not simultaneous (fig. 8). Further divisions may also occur, resulting in the formation of more than 4 microspores from a single mother cell, as many as 6 having been found (figs. 9–12). The microspores soon separate from one another and become surrounded by moderately heavy spore coats (fig. 13), the tapetum remaining quite prominent and showing little signs of disintegration even at this time. The microspore stage is the winter condition of the microsporangium, the only noticeable change in the microspores between this and pollination being an increase in size (figs. 13, 14). This growth takes place in the early spring, during the period in which the strobilus is emerging from the winter scales and attaining its mature size (about the middle of April).

Torreya californica in England (**10**) and *T. taxifolia* in Florida (**14**) pass the winter in the mother cell condition. STRASBURGER (**12**) reports that in *Taxus baccata* the "pollen mother cells" divided, in 1904, during unusually warm weather in February. So far as reported, *T. canadensis* is the only one of the Taxineae passing the winter in the microspore stage, the microspore mother cell or earlier being the more usual winter condition of our north temperate gymnosperms.

The pollen grain is uninucleate (fig. 14) when shed and shows no indications of prothallial cells, this agreeing with *T. baccata* as reported by several workers (BELAJEFF **3**, JÄGER **6**, and COKER **9**). Among the other Taxineae, *Torreya* (**14**) and *Cephalotaxus* (**4**, **16**,

17) are binucleate when shed, the microspore having divided into the tube and generative cells while in the microsporangium. The absence of prothallial cells is a feature common to the Taxineae, Taxodineae, and Cupressineae.

POLLINATION.—In the spring of 1914, in the vicinity of Huntingdon, Pennsylvania, pollination was first noted April 23. No strobili were found shedding pollen on April 20, but 3 days later pollen was being shed abundantly, especially in the more exposed situations, and most of the ovules collected at that time contain pollen grains. JÄGER (6), at Zurich, reports the beginning or middle of March as the time for the pollination of *T. baccata*.

The pollen grains are wind scattered and are formed in great abundance, while the frequent occurrence of both staminate and ovulate strobili on the same shoot increases the chances for pollination. In the material which I have examined there were very few ovules which had not been pollinated, and sometimes quite abundantly, as is evidenced by the frequency of several pollen tubes in an ovule. The pollen is caught by the small pollination droplet which protrudes from the micropyle of the ovule and is drawn into the micropyle by the concentration of the droplet.

In the ovule the pollen grains are found on the upper end of the nucellus. While no definite pollen chamber is formed, the outermost cells of the nucellus begin to disintegrate about the time of pollination, resulting in a ragged edge to the nucellus on which the pollen grains become lodged.

POLLEN TUBE.—The pollen grain, lying on the nucellus, soon begins to elongate, the exine is ruptured, and the intine grows out to form the tube. The young tube soon penetrates the nucellus, and, once started, invades the tissue very rapidly. Within a week or 10 days some of the tubes have reached the female gametophyte, while others may not have penetrated so far, there being considerable variation in this respect even in a single ovule, although the rapid growth is the more general situation (figs. 16–20, 22).

The general course of the pollen tube is toward the region of the female gametophyte, which occupies the center of the nucellus. However, it is not uncommon for tubes to penetrate the nucellus

nearer its margins, in some cases reaching close to the edge of the nucellus (fig. 27). During the elongation of the tube there is also considerable increase in diameter, such that by the time the tube has reached the female gametophyte region its diameter is several times greater than at first (fig. 22). A striking enlargement now takes place. If the female gametophyte still consists of free nuclei, as it frequently does at this time, it may be so crowded upon by the enlarging tube as to be pushed to one side; or the megaspore membrane may remain quite firm, retaining its shape, the tube then being forced to conform its shape to that of the resisting megaspore membrane (fig. 28). A number of cases of branching tubes were found, the nuclear contents in such cases being near the point of branching, while the branches generally have dense cytoplasmic contents, indicating their haustorial activity. The enlarging tube usually spreads itself over the micropylar end of the female gametophyte; it may go off to one side and penetrate far into the nucellus; or it may grow along the side of the endosperm, passing by the archegonia in the micropylar end of the endosperm. If two female gametophytes are formed in an axial row, the pollen tube usually enlarges between them, while in some cases the pollen tube may entirely pass the developing female gametophyte and enlarge below it. It seems that in such cases the female gametophyte is developing from an upper megaspore (fig. 31).

In case the nucellus is invaded by a number of tubes they produce a rather interesting situation. The female gametophyte is crowded upon from several sides and is frequently pressed quite out of its normal shape. A case was found of an ovule which has no fewer than 22 pollen tubes, as indicated by their nuclear contents (fig. 32). The pollen tubes have completely invested the endosperm, considerably distorting it, and possibly preventing its normal development, although young archegonia are recognizable in it. In another case at least 9 tubes had enlarged about the endosperm, practically surrounding it, but in this case 3 of the archegonia had been fertilized and proembryos formed within them.

Apparently the tubes do not fuse even when in contact with one another, although when there are a number of tubes in an ovule

their enlargement and crowding upon one another produces such a complex that it is practically impossible to count the tubes except by their nuclear contents. The tubes which are on the periphery of the complex may be so crowded by the more interior ones as to remain quite narrow and their contained body cells may even be flattened by the pressure.

The cytoplasmic contents of the tube become quite vacuolated early in the growth of the tube and in early stages contain a large number of starch grains, although these apparently disappear in the later stages. The cytoplasm is always more abundant near the growing end of the tube, but when the tube enlarges at the forward end the bulk of the cytoplasm remains more or less closely connected with the nuclei of the male gametophyte. Frequently in late stages the cytoplasm may contain accumulated masses, irregular in shape and densely staining, and these may even be discharged into the egg cytoplasm at the time of fertilization.

DEVELOPMENT OF MALE GAMETOPHYTE.—Soon after pollination the microspore begins to elongate, and the first division into tube and generative cells takes place within 10–12 days after pollination (fig. 16). This division results in two unequal cells (fig. 17), the smaller generative cell being held in the base of the grain by a plasma membrane, while the larger tube cell forms the elongating tube. The division of nuclear material is no doubt equal, but the tube cell nucleus soon becomes larger than the nucleus of the generative cell, the former becoming ellipsoid and retaining this shape throughout the remainder of its history. The cytoplasm of the generative cell is denser than that of the tube cell.

As the tube elongates, the tube cell nucleus passes into the growing end, migrating rapidly behind the tip of the tube (figs. 19, 20). Even before the generative cell divides, the tube cell nucleus has usually gone some distance into the tube. The generative cell enlarges, pushes out its limiting membrane, and then divides. No case was found showing the second division, but that the two nuclei found together in the basal part of the tube (fig. 20) arose from the division of the generative cell can hardly be doubted. The basal one, the stalk cell, has a more vacuolated cytoplasm than that of the anterior body cell.

The body cell soon migrates into the tube and is followed by the stalk cell nucleus, the two usually being in contact and apparently having passed into the tube together. During the growth of the tube through the nucellus, up to the time when the pollen tube reaches the female gametophyte, the 3 nuclei are in an axial row, while later the stalk nucleus migrates around the body cell and takes a position besides the tube nucleus. Of these two nuclei in the tube, the tube nucleus is generally to be recognized by its being slightly larger than the stalk nucleus. The body cell begins enlarging at once after entering the tube. As it passes down the tube it is slightly ellipsoid, but on reaching the end of the tube, as the latter is enlarging about the endosperm, it becomes rounded as it increases in size. The cytoplasm remains dense and the nucleus becomes large. During the early history of the body cell its cytoplasm is uniformly distributed through the cell, but as it reaches its mature size the cytoplasm becomes less dense along the periphery and here shows delicate radial strands (fig. 23). The nucleus, which earlier occupied a central position, takes a more peripheral one (usually on the side opposite to that on which the stalk and tube nuclei lie), while the cytoplasm becomes considerably vacuolated along the margin of the cell, the radial strands disappearing with the increased vacuolization.

The division of the body cell into the two male cells takes place shortly before fertilization. Several mitotic figures of this division were found. The nucleus of the body cell being at one side of the cell, there is an unequal division of the cytoplasmic material. A broad spindle is formed and the cell plate laid down on it is lenticular in outline, resulting in the formation of the two unequal male cells, a small lens-shaped cell and a larger more rounded one. The nucleus of the larger cell takes a central position and enlarges, while with the growth of the nucleus of the smaller cell the latter soon has the appearance of a naked nucleus invested only by the nuclear membrane, the two cells remaining in contact with one another and being held together by the plasma membrane of the parent body cell (figs. 23–26). What is probably a similar situation in *Taxus baccata* has given rise to differences in the accounts as given by different workers. BELAJEFF (3) could not find a plasma

investment of the smaller nucleus. He speaks of "male nuclei" and not of male cells. His figure shows two nuclei in a common cytoplasmic mass. STRASBURGER (4) and JÄGER (6) both recognized two "cells." Miss ROBERTSON (18) figures the division of the body cell, but no cell plate is shown on the spindle, even in the late telophase; while her figure of the completed division lacks clearness on this point, owing to a possible inaccuracy in drawing or in technique. In her discussion she speaks of a "functional male nucleus" and "inequality of the sperm nuclei."

By the time the two male cells are formed, the vacuolization along the margin of the larger cell has become quite pronounced (fig. 26), and this continues until finally the cytoplasm has practically all withdrawn from the plasma membrane and collected about the nucleus. In this condition the male gametophyte has reached its maturity and fertilization may now take place. Should male cells fail to function in fertilizing an egg, as is frequently the case where there are a number of tubes in an ovule, they remain in this condition for a time and then disintegrate. Male cells have been found in ovules in which the proembryo was considerably advanced.

Two unequal male cells are reported for *Torreya taxifolia* (14) and *Cephalotaxus Fortunei* (16), and the division of the body cell into male nuclei in *C. drupacea* (17). Miss ROBERTSON concludes that there are formed "a functional male nucleus" and a "smaller male nucleus" in *T. californica* (18). In an earlier account (11) she had stated that the body cell divided into two nuclei of equal size. There is evident among the Taxineae a tendency toward the elimination of male cells in the formation of the so-called "male nuclei" only. The inequality of these nuclei or cells is another advance. A mere cutting off of the smaller nucleus from the body cell would be another step; while the final one, not known to be reached by any of the gymnosperms, would be a body cell functioning as a male cell. In *Taxus* the male gametophyte at its maturity consists of the stalk and tube nuclei and the two male cells. This is interesting in comparison with the angiosperm situation, in which the generative cell in its division produces the two male cells directly, thus eliminating one more

division between the microspore and the cells functioning in fertilization.

Female gametophyte

MEGASPORES.—STRASBURGER (2) long ago pointed out that in *Taxus baccata* the megaspore mother cells are the end cells of a series arising from the hypodermal layer of the nucellus, and that they are clearly distinguished from the surrounding cells by their larger size and larger nuclei. The same situation seems to hold for *T. canadensis*. STRASBURGER (2) claimed several megaspore mother cells; JÄGER (6) agrees with him, but COKER (9) in his study of *T. baccata* states that there is no evidence that more than one megaspore is ever formed. He says "the mother cell is hard to distinguish. At the time of its first division it is long and narrow, resembling very closely the cells adjoining." As to the number of mother cells, STRASBURGER was probably right. In my preparations I have found no difficulty in recognizing the megaspore mother cells, nor does there seem to be any doubt that there may be a number of them in an ovule. Only one, or occasionally two, may function, but other megaspore mother cells may be present, by all the other tests of a mother cell. The mother cells are distinguished from the other cells of the nucellus, not only by their size and the size of their nuclei, but by their different staining reaction. The group of mother cells may be recognized in the autumn or winter (fig. 33). The occurrence of two linear tetrads of megaspores (fig. 38) is sufficient evidence that there have been at least two megaspore mother cells in the case figured.

STRASBURGER (12) and COKER (9) have given rather complete descriptions of megaspore formation in *Taxus baccata*, and the process is essentially the same in *T. canadensis*, so far as my preparations show (figs. 34–38). In *T. baccata* the second division is said to be simultaneous in both daughter cells. This is probably the case in *T. canadensis* in most instances, although one case was found in which the division of the upper cell was completed before that of the lower (fig. 36).

Starch is present in considerable abundance in the megaspore mother cells as well as in the neighboring cells, and it is also found in the megaspores and in the developing female gametophyte.

STRASBURGER (12) states that the starch soon disappears from the megaspore mother cells of *T. baccata*, but COKER (9) in his figures shows starch grains in the megaspores as well as in the megaspore mother cells. The starch is not confined to the megaspore region, but is found abundantly in the adjoining cells, and some of it occurs throughout a considerable portion of the nucellus in *T. canadensis*.

The method of formation of a tapetum about the megaspore mother cells, as pointed out by STRASBURGER (12) in *T. baccata*, also holds for *T. canadensis*. These cells are formed more or less obliquely to the long axis of the megaspore cells (fig. 34), are rich in content, and stain differently from the megaspore mother cells. THOMSON (15) speaks of the tapetum derived from the nucellus as a "secondary tapetum," in distinction from forms in which the tapetum is derived from the sporogenous tissue. in which case it is called a "primary tapetum." GOEBEL pointed out long ago, however, that the significance of the "tapetum" is physiological, and not morphological, and that it may have a variety of origins. The megaspore mother cell seems to be the usual winter condition. While STRASBURGER (12) says the megaspore mother cells of *T. baccata* are completed in October and that further development takes place the next spring, this does not always hold for *T. canadensis*, as I have found young female gametophytes of several free nuclei in some of the material collected in November, 1913. Most of the ovules taken at this time showed the mother cell condition, but even in some of the ovules collected as late as December it may be doubted whether the megaspore mother cells had become fully matured. Evidently, therefore, the time for the maturity of the megaspore mother cells and the formation of megaspores may vary, yet the general statement may be made that the mother cell is the usual winter condition and that megaspore formation generally takes place in the spring with the renewal of the growing season.

Usually the innermost one of the linear tetrad of megaspores is the functional one, the 3 outermost then disorganizing and disappearing sooner or later (fig. 39). Any of the megaspores may function, however, as 1, 2, 3, or even all 4 of the megaspores may grow after their formation and more than one may divide in

the formation of young female gametophytes (figs. 39–44). The further development of several megaspores will be described later. Some interesting cases were found, such as those in which one of the upper megaspores had evidently functioned, while the lower ones had failed to develop, although still recognizable (figs. 30, 31). In both cases figured the pollen tubes have pushed past the gametophytes and penetrated to the central region of the nucellus.

THOMSON (15) in his investigation covering the megaspore membrane situation in the gymnosperms reports that in *Taxus canadensis* the megaspore membrane, while recognizable in the early free nuclear stages of the gametophyte, is practically unrecognizable in later stages. This agrees with my observations that the membrane is quite firm about the young female gametophyte, but seemingly fails to develop with the endosperm and is soon lost sight of. THOMSON associates this with the absence of the "primary tapetum" and regards it as a specialized advanced character, indicating that the Taxineae are "recent" as compared with some other forms.

DEVELOPMENT OF FEMALE GAMETOPHYTE

Free nuclear stage.—The first division of the functional megaspores takes place soon after their formation, and other divisions, which are always simultaneous, follow in rapid succession (figs. 39, 45, 46). The embryo sac enlarges as the number of nuclei increases. At first the nuclei are scattered in the embryo sac. but as this increases in size it becomes vacuolated in the center, the cytoplasm with the nuclei then taking a peripheral position, this condition being attained when the 8 or 16-nucleate stage is reached (figs. 47, 48). As reported by JÄGER (6) for *Taxus baccata*, about 8 successive divisions occur, resulting in approximately 256 free nuclei before wall formation takes place. The vacuole in the embryo sac has kept pace with the growth of the sac and the nuclei occur in the narrow cytoplasmic layer along the periphery, the cytoplasm not being uniformly distributed, however, but showing distinct radiations connecting the nuclei when seen in a tangential view (fig. 49).

In the enlargement of the embryo sac, if a lower megaspore is functioning, the growth seems to be downward; if an upper megaspore is functioning, the growth is upward; if two gametophytes

are developing, one grows upward, the other downward (fig. 51). In the early stages the embryo sac is usually pear-shaped, the narrow portion marking the original position of the megaspores, while the expanded portion shows the region of growth (figs. 47, 51). The growth of the embryo sac and the enlargement of the endosperm after walls have been formed crowd upon the adjoining cells of the nucellus in such a way as to distort and flatten them, while no doubt some of the nucellar tissue is also digested by the growing gametophyte.

Wall formation and growth of endosperm.—The first formation of walls between the nuclei results in a single layer of cells surrounding the central cavity (fig. 50). The cells at this stage are rich in starch, the starch grains having also been present during the free nuclear stages. Centripetal growth of these cells then begins by the radial lengthening of their walls, the walls reaching the center and forming a completely closed tissue before further cell division takes place. Several cases were found showing this feature in various stages, but in no case had periclinal walls formed before the tissue was closed (fig. 51). Cells which in a single section appear to be internal are merely the inner ends of cells abutting the margin in other sections. At the very narrow upper end the cells are very closely crowded together.

JÄGER'S account (6) of the formation of the endosperm in *Taxus baccata* differs in a few details from this, in that he states that the cavity is filled with tissue by the inward growth of a series of cells formed by periclinal walls. His technique was such, however, that he could easily have been mistaken in his interpretation of the situation. The filling of the central cavity by growth and periclinal divisions seems to be the rule among gymnosperms, and is probably to be correlated with the size of the cavity at the time wall formation begins. The smallness of the cavity in *Taxus* may account for the method of tissue formation found here.

Following the complete filling of the central cavity with cell tissue, periclinal walls come in, giving rise to several layers of cells between the margin and the center. Anticlinal divisions also take place soon and the growth of the endosperm in all directions continues. Archegonia soon appear in the micropylar end of the tissue.

Growth of the endosperm goes on rapidly, the greater meristematic activity being in the central portion, especially in the basal region. In the early history of the endosperm the cells are uninucleate, but as the embryo develops they become multinucleate, while in the central portion of the endosperm, below the growing tip of the embryo, the cells become elongated, forming a conducting tract for the food from the basal region of the ovule to the growing embryo. This elongation ceases to show after the embryo reaches maturity. In the mature endosperm, with the exception of the extreme micropylar portion, an abundance of food material is stored, this being the food supply of the seedling in the early stages of its germination.

A comparison of the size of the endosperm at different times in its development may be of interest. In fig. 52 there are shown 3 outline drawings, to the same scale, showing the comparative size of the endosperm at the time of wall formation (as in fig. 51), at the time of fertilization, and at the maturity of the seed. It is readily seen that the greatest growth of the endosperm takes place after fertilization.

Archegonia.—The archegonium initial arises from the outermost layer of cells and is recognizable very shortly after periclinal walls come in. The initials appear a short distance behind the "point" of the endosperm, but always occur in the micropylar end if the gametophyte is one which has developed from an inner megaspore; in case of a gametophyte from an outer megaspore the archegonia will be on the side of the gametophyte toward the center of the ovule. The initials can be recognized by their slightly larger size and by the size of their nuclei (fig. 53). The surrounding cells form the archegonial jacket. The initial divides into the primary neck cell and the central cell (fig. 54). The primary neck cell divides into several neck cells, all in the tangential plane, serving merely as a covering for the central cell, a "neck" hardly being recognizable. These neck cells become flattened, and by the time of the maturity of the archegonia are mere plates, usually with degenerate nuclei and but little cytoplasm.

The central cell enlarges to the mature size, and since in the large number of archegonia examined there were no indications of a

ventral canal cell or nucleus, it may be regarded that this central cell is the functional egg. This agrees with *Torreya taxifolia* (14). In *Cephalotaxus Fortunei* (15) and *C. drupacea* (16) a ventral nucleus is formed, in the latter disorganizing before fertilization. This marks the final elimination of the row of canal cells, an elimination which has been such a persistent and gradual process from bryophytes through pteridophytes and gymnosperms.

In the earlier stages of the archegonium the central cell nucleus is near the upper end of the cell, but as the archegonium matures it takes a more central position (fig. 55), the cytoplasm being somewhat vacuolated and supplied with an abundance of food material, some of which stains quite darkly with the staining agents used.

The archegonial jacket is recognizable from the initial to the mature archegonium, but is not strikingly conspicuous as in some other forms, and less so in the mature condition than earlier. Usually there is a jacket about each archegonium, with several layers of cells between the archegonia, but it is not a rare thing to see two archegonia with only a single layer of jacket cells between them, and several cases were found in which two archegonia were surrounded by a common jacket, this latter condition being an approach to the archegonium complex found in some of the other groups of gymnosperms. Several archegonia are usually present in a gametophyte, 4–8 being the average number.

SUPERNUMERARY GAMETOPHYTES.—Mention has been made of the fact that more than one megaspore may function. HOFMEISTER (1) long ago pointed out the presence of more than one embryo sac in *Taxus baccata*, and JÄGER (6), STRASBURGER (12), and Miss ROBERTSON (18) have found the same situation. STRASBURGER states that usually one embryo sac develops; if more than one starts, one is usually suppressed; but several times he observed two equally strong embryo sacs with more or less free peripheral nuclei, the two embryo sacs usually lying beside one another, and one case of one above the other. COKER (9) and THOMSON (15) found more than one embryo sac in *T. canadensis*, the former stating that one of the two gametophytes is smaller than the other, and while both may bear archegonia, the archegonia in the upper gametophyte face the pollen tube which has pushed in between the

two gametophytes, only the archegonia of the lower gametophyte, however, being fertilized.

In my material I find two gametophytes quite common, usually in an axial row, although sometimes lying side by side (fig. 57). One is usually larger than the other, the upper generally being the smaller of the two, and both may produce archegonia, as pointed out by COKER. Usually when 2 gametophytes develop in an axial row the pollen tubes push in between them, and then the archegonia are directed toward the tubes; but this is not always the case, as sometimes there are 2 apparently equally vigorous gametophytes, one above the other, and both with good archegonia in their micropylar ends. The pollen tube has spread out above the upper gametophyte, while the lower one is not in contact with the tube at any point in the case shown in fig. 58.

Several instances of more than 2 gametophytes in an ovule were found. One case (fig. 59) shows 3 gametophytes with tissue, the pollen tube lying between the two uppermost. No archegonia were present in the upper one, but both of the lower ones have good archegonia, one of which has been fertilized and contains a proembryo. Other cases show 4 gametophytes, in one of which (fig. 60) 2 of the gametophytes have formed tissue, while the other 2 are in free nuclear condition, archegonia being present only in the lowest, which also contains a proembryo, the pollen tube in this case having pushed its way between the 4 gametophytes. In another case (fig. 61) the ovule contains 3 gametophytes with tissue and archegonia, while the fourth one consists of only a few free nuclei and, although lying between two vigorous gametophytes with tissue, retains its shape, evidently owing to the firmness of the megaspore membrane. One ovule was found containing 5 gametophytes, 3 with free nuclei and 2 with tissue (fig. 62), only the lowest of the 5 having developed an archegonium. In this case more than one megaspore mother cell must have functioned. With two tetrads of megaspores (fig. 38) a situation such as this, and even with more gametophytes, is not impossible.

The mechanics by which the developing gametophytes become separated by the enlarging tube might be an interesting problem,

to which it may be suggested that there is an elongation of the nucellus during the growth of the gametophytes, together with a digestion of that portion of the nucellus immediately adjacent to them. The megaspores were evidently in contact when formed, but by the enlargement of the pollen tube between the young gametophytes they become widely separated as the tube develops.

Fertilization

While the fertilized egg represents a new phase in the life history and the account of it might be more properly included with that of the embryogeny, it may not be out of place to give a brief account of it in this connection. Ovules containing proembryos were found in material collected May 21. Preparations showing fertilization were found from this time on to as late as the middle of June, showing that the time for fertilization is not constant and may have considerable range.

At the time of fertilization the neck of the archegonium becomes ruptured and the nuclear contents and part of the cytoplasmic contents of the tube are discharged into the egg. The egg nucleus has migrated to the basal portion of the egg; the male nucleus with its investing cytoplasm comes in contact with the egg nucleus; the cytoplasm of the male nucleus invests the two nuclei lying in contact and forms a dense sheath about them (fig. 56). With the fusion of the two nuclei the act of fertilization is complete. The behavior of the chromatin in fertilization could not be determined from my material. The cytoplasmic sheath about the two nuclei also occurs in *Torreya californica* (11), *T. taxifolia* (14), and *Cephalotaxus Fortunei* (16) among the Taxaceae, as well as in several other cases reported, namely, by COKER (8) in *Taxodium;* by LAND (13) in *Ephedra;* and by NICHOLS (19) in *Juniperus communis* var. *depressa*.

The smaller male cell and the stalk and tube nuclei, together with the densely staining mass of the tube cytoplasm, when present, usually remain in the upper portion of the egg, where they sooner or later disorganize, although they may persist for some time and be recognizable at somewhat late stages of the proembryo or even after the suspensors have begun to elongate.

Time relations

The time periods involved in the reproductive process are always of interest in the gymnosperms, as use is made of this feature in determining the primitive or modern character of a group, those having short periods being regarded as the more advanced in this respect. In my material the time from microspore formation to pollination was about 6.5 months; from pollination to fertilization may be as short as one month, although fertilization generally occurs after a longer interval, the time between pollination and fertilization having a considerable range, with an accompanying range in the time of the maturity of the seed. I have collected mature seeds from the first week of July until late in September in central Pennsylvania. BELAJEFF (3) shows a pollen tube of *Taxus baccata* with two nuclei collected April 10 and a figure of fertilization dated May 26. JÄGER (6), at Zurich, reports pollination at the beginning or middle of March and fertilization at the end of May or beginning of June. Miss ROBERTSON (18) reports the time for fertilization at Kew to be about the middle of June. STRASBURGER (4) speaks of fertilization taking place the first half of July and the embryo complete by the end of August. None of these accounts gives so short a time period as I have found for *T. canadensis*.

Summary

Microspore formation takes place in the autumn. There are no indications of prothallial cells. The pollen grain is uninucleate when shed.

The pollen tube penetrates the nucellus very rapidly and enlarges excessively about the female gametophyte.

Three divisions take place in the development of the male gametophyte. The body cell divides into two unequal male cells, the larger of which functions in fertilization.

Several megaspore mother cells are formed, of which only one usually functions, although two of them may form megaspores. The megaspore mother cell is the usual winter condition, but megaspores may be formed and the female gametophyte may consist of several free nuclei before winter.

Following the free nuclear stage of the female gametophyte, radical walls come in, closing the cavity before the appearance of periclinal walls.

The archegonia appear early in the endosperm. The central cell is the functional egg, no ventral canal cell or ventral nucleus being formed.

More than one female gametophyte in an ovule is common; as many as 5 were observed.

In fertilization the nuclear contents of the pollen tube are discharged into the egg. A cytoplasmic sheath is formed about the two fusing nuclei.

From pollination to fertilization may be as short as one month. Mature seeds have been collected 6 weeks later.

In general the gametophyte history agrees with that reported for *T. baccata*.

The writer takes pleasure in acknowledging obligations to Professors JOHN M. COULTER and C. J. CHAMBERLAIN, under whose direction the study was made.

BRIDGEWATER, VA.

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EXPLANATION OF PLATES XI–XIV

All drawings were made with a camera lucida and the figures illustrating a series of processes are drawn to the same scale in order to show comparative sizes. The original drawings are here reduced one-half. The magnification of the figures is approximately as follows: figs. 1–21, 23–26, ×570; fig. 22, ×92; figs. 27–32, 57–62, ×57; figs. 33–51, 53–56, ×268.

PLATE XI

FIG. 1.—Group of megaspore mother cells.

FIG. 2.—Synapsis preceding reduction.

FIGS. 3–7.—Stages in reduction division.

FIG. 8.—Two microspores are formed; second division in formation of other two not yet completed.

FIG. 9.—Complete tetrad of 4 microspores.

FIGS. 10–12.—Tetrads of more than 4 microspores, fig. 12 showing 6 microspores.

FIG. 13.—Portion of a microsporangium, showing wall, tapetum, and several microspores in winter condition.

FIG. 14.—Mature microspore at time of shedding.

FIG. 15.—Pollen grain after pollination has taken place, beginning to elongate.

FIG. 16.—First division of microspore.

FIG. 17.—Smaller generative cell and larger tube cell resulting from first division of microspore.

FIG. 18.—Stage slightly more advanced than preceding figure; tube nucleus passing into tube and cytoplasm becoming vacuolated.

FIG. 19.—Somewhat older tube, showing generative cell in forward end of tube enlarging before division, and large number of starch grains in cytoplasm of tube.

FIG. 20.—Generative cell has divided into basal stalk cell and anterior body cell, which already shows denser cytoplasmic contents than stalk cell.

FIG. 21.—Passage of stalk and body cells into tube.

FIG. 22.—Portion of an ovule (reconstructed from several sections) showing female gametophyte in nucellar tissue and several pollen tubes which have penetrated nucellus to female gametophyte.

FIG. 23.—Body cell at time of maturity, with laterally placed nucleus and delicate cytoplasmic radiations along periphery, together with stalk cell nucleus and tube nucleus.

FIG. 24.—Division of body cell.

FIG. 25.—Late stage in division of body cell; lenticular cell plate is shown, as well as vacuolization along margin of cell.

FIG. 26.—Mature male gametophyte, consisting of two unequal male cells, stalk cell nucleus, and tube nucleus.

PLATE XII

FIG. 27.—Portion of an ovule in which a branching pollen tube has passed to one side of nucellus.

FIG. 28.—Portion of an ovule showing more usual relation of pollen tube to female gametophyte.

FIG. 29.—Portion of an ovule in which pollen tube has passed to one side of female gametophyte, penetrating nucellus nearly to base of female gametophyte.

FIG. 30.—Portion of an ovule in which female gametophyte has developed from an upper megaspore, pollen tube having pushed past gametophyte.

FIG. 31.—Two pollen tubes have pushed past female gametophyte and enlarged below it; non-functioning lower megaspore is recognizable.

FIG. 32.—An ovule which contained no less than 22 pollen tubes; the figure is a reconstruction of several sections and shows the complex about female gametophyte and nuclear contents of several tubes.

FIG. 33.—Group of several megaspore mother cells.

FIG. 34.—Synapsis preceding reduction division of megaspore mother cell; division showing method of formation of tapetum.

FIG. 35.—The 2 cells resulting from first division of one of the two megaspore mother cells.

FIG. 36.—Megaspore tetrad, division of two lowest as yet incomplete.

FIG. 37.—Linear tetrad of megaspores.

FIG. 38.—Two linear tetrads of megaspores.

FIG. 39.—Innermost megaspore dividing, 3 outer ones degenerating.

FIG. 40.—Two-celled female gametophyte from division of inner megaspore; second megaspore has enlarged.

FIG. 41.—Inner megaspore divided, other 3 showing no signs of disintegration.

PLATE XIII

FIG. 42.—Four megaspores have enlarged considerably and nucleus of one has divided.

FIG. 43.—Second of the 4 megaspores has divided; first has enlarged somewhat, the two innermost retaining their normal size and appearance.

FIG. 44.—Third and fourth megaspores have each divided twice, second megaspore has enlarged, while outer one is beginning to degenerate.

FIG. 45.—Second division of megaspore.

FIG. 46.—Third division of megaspore; note beginning of formation of pear-shaped embryo sac.

FIG. 47.—An 8-nucleate female gametophyte.

FIG. 48.—Group in which first and third megaspores are disintegrating, second has enlarged considerably, while the fourth has produced an 8-nucleate female gametophyte.

FIG. 49.—Tangential view of a few nuclei and connecting cytoplasmic strands in free nuclear condition of female gametophyte.

FIG. 50.—Female gametophyte showing single layer of cells following first wall formation.

FIG. 51.—Two female gametophytes in axial row; upper one in free nuclear condition, lower with tissue just completed, completely closing embryo sac cavity; no periclinal walls have appeared, cells showing in interior being merely portions of cells whose outer ends abut on margin.

FIG. 52.—Female gametophyte at 3 different stages, at time of complete closing of cavity (fig. 51), at time of fertilization, and at maturity of seed, drawn to same scale, to show comparative size at different stages.

PLATE XIV

FIG. 53.—Upper portion of a female gametophyte showing 2 archegonium initials.

FIG. 54.—Two archegonia, showing young central and primary neck cells.

FIG. 55.—Mature archegonium; nucleus has become centrally placed, cytoplasm shows more or less radiations from nucleus and contains considerable food material; nuclei of neck cells degenerating.

FIG. 56.—Fertilization: male nucleus and egg nucleus are in contact at base of egg, surrounded by cytoplasmic sheath; smaller male cell nucleus and tube and stalk cell nuclei can be seen in upper portion of egg cytoplasm; ellipsoid dark bodies are food particles, while irregular dark mass seen in upper portion of egg is an accumulated mass of cytoplasm from pollen tube.

FIG. 57.—Two female gametophytes lying side by side, with innermost portions of 2 pollen tubes beside them.

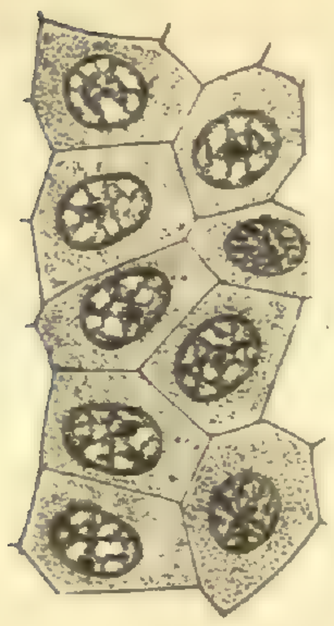
FIG. 58.—Two gametophytes in axial row, both having developed good archegonia; pollen tube has spread out over micropylar end of outer gametophyte.

FIG. 59.—Three female gametophytes in axial row, with pollen tube between first and second; second contains a proembryo, while inner one also contains a good archegonium.

FIG. 60.—Ovule containing 4 female gametophytes, 2 of which are in free nuclear condition; lower one contains a proembryo; pollen tube has crowded between the 4 gametophytes.

FIG. 61.—Another ovule with 4 female gametophytes, 3 of which contain archegonia; one of gametophytes consists of only a few free nuclei, but has not been pressed out of shape by its neighbors; pollen tube is shown below upper gametophyte.

FIG. 62.—Portion of ovule with 5 female gametophytes, 3 of which are in free nuclear condition, and an archegonium appearing only in lower of two with tissue; enlarging pollen tube has widely separated 3 upper gametopnytes from 2 lower ones.



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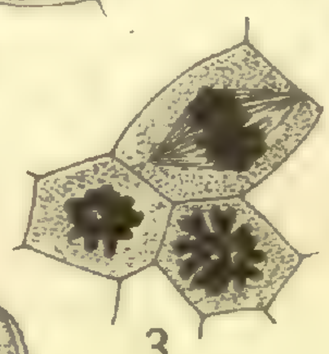

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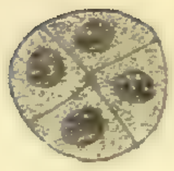

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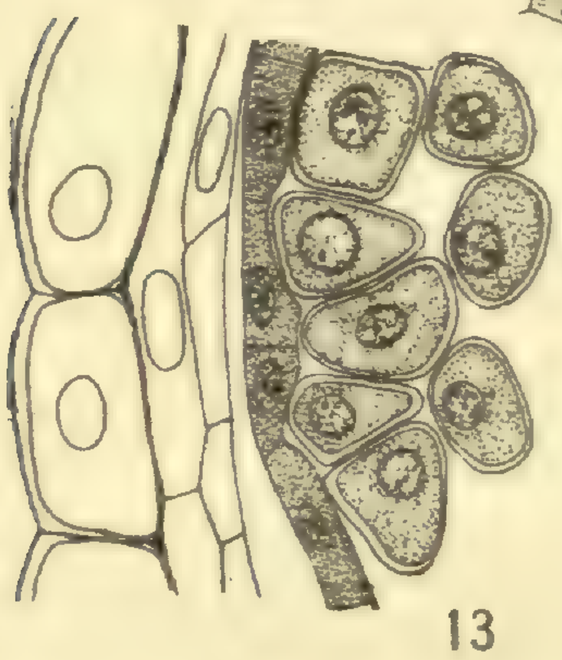

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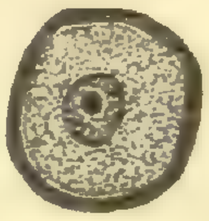

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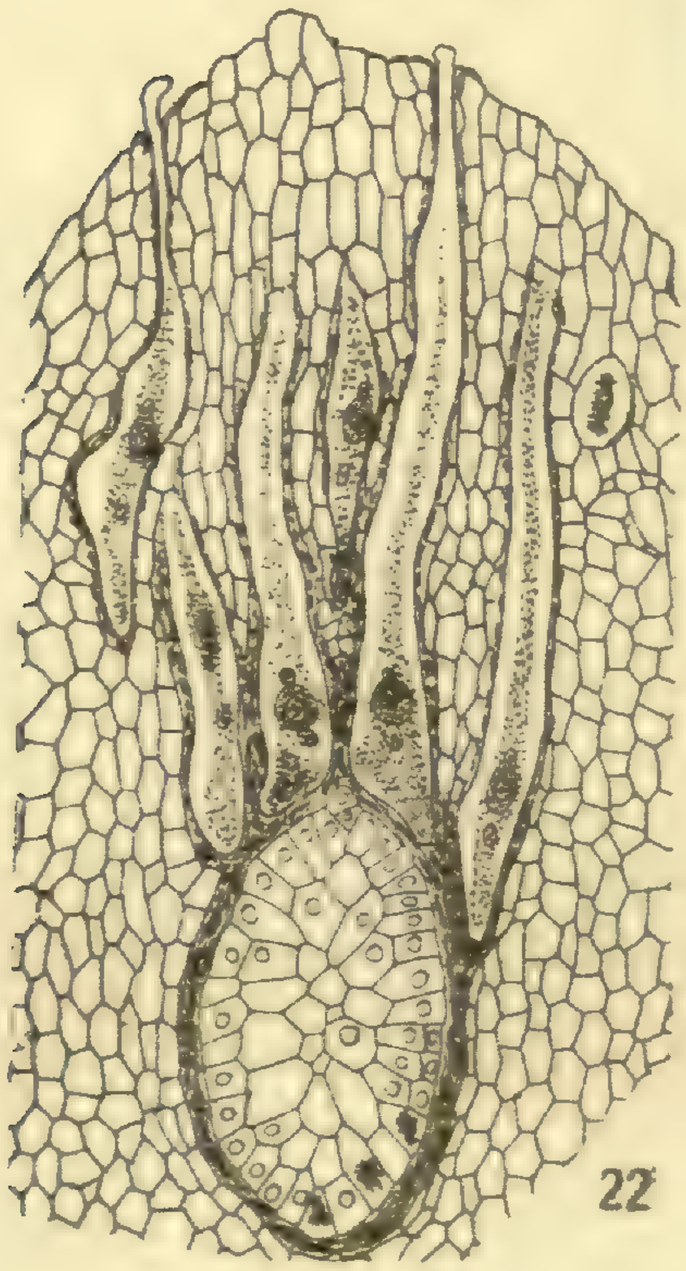

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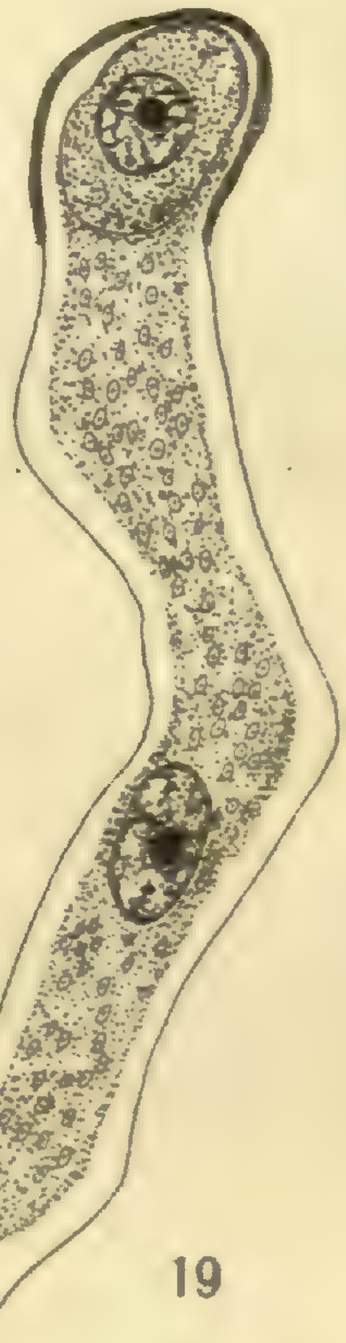

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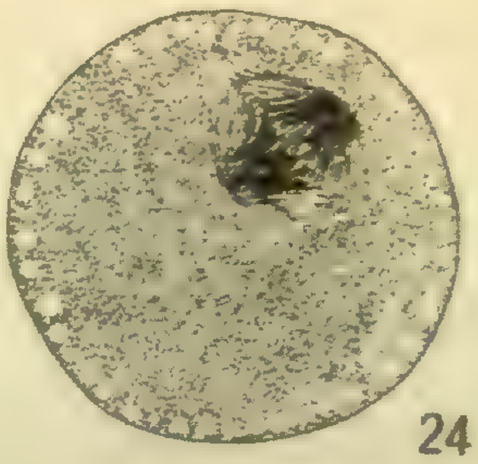

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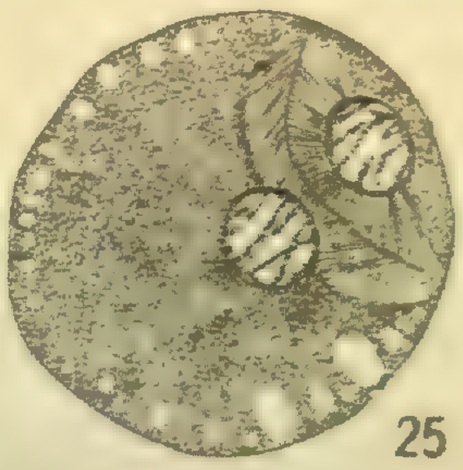

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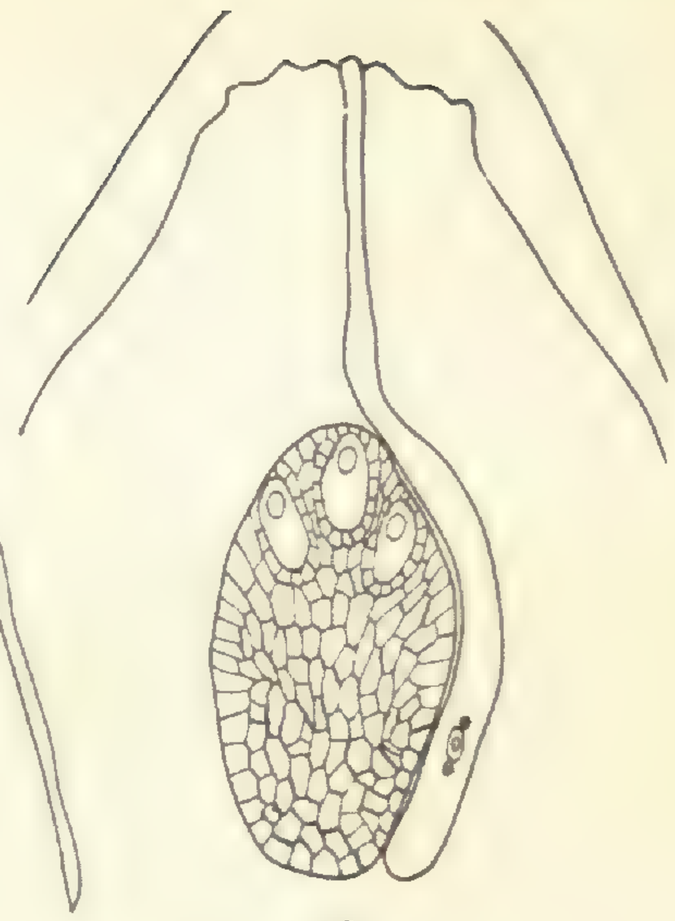
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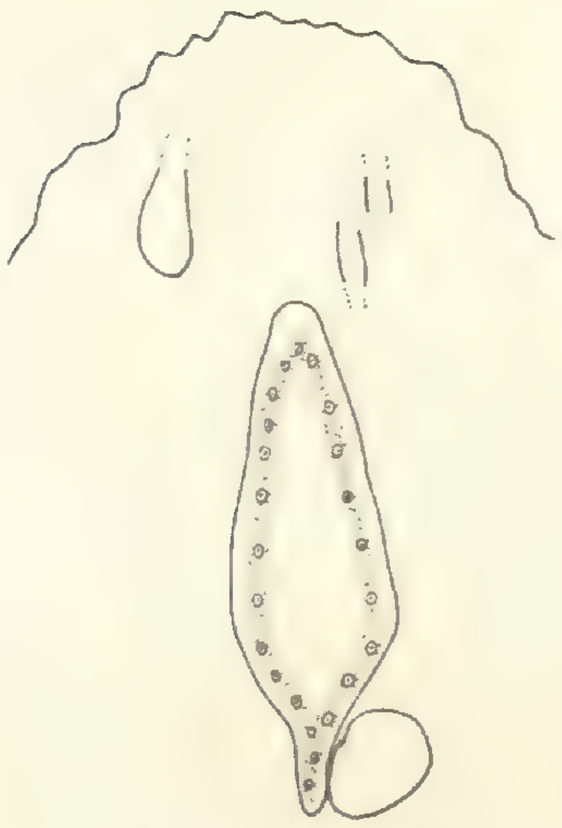
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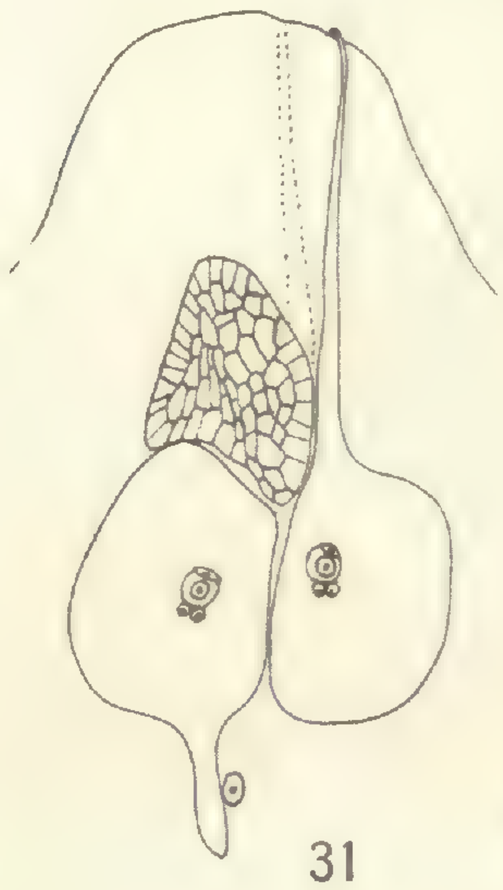
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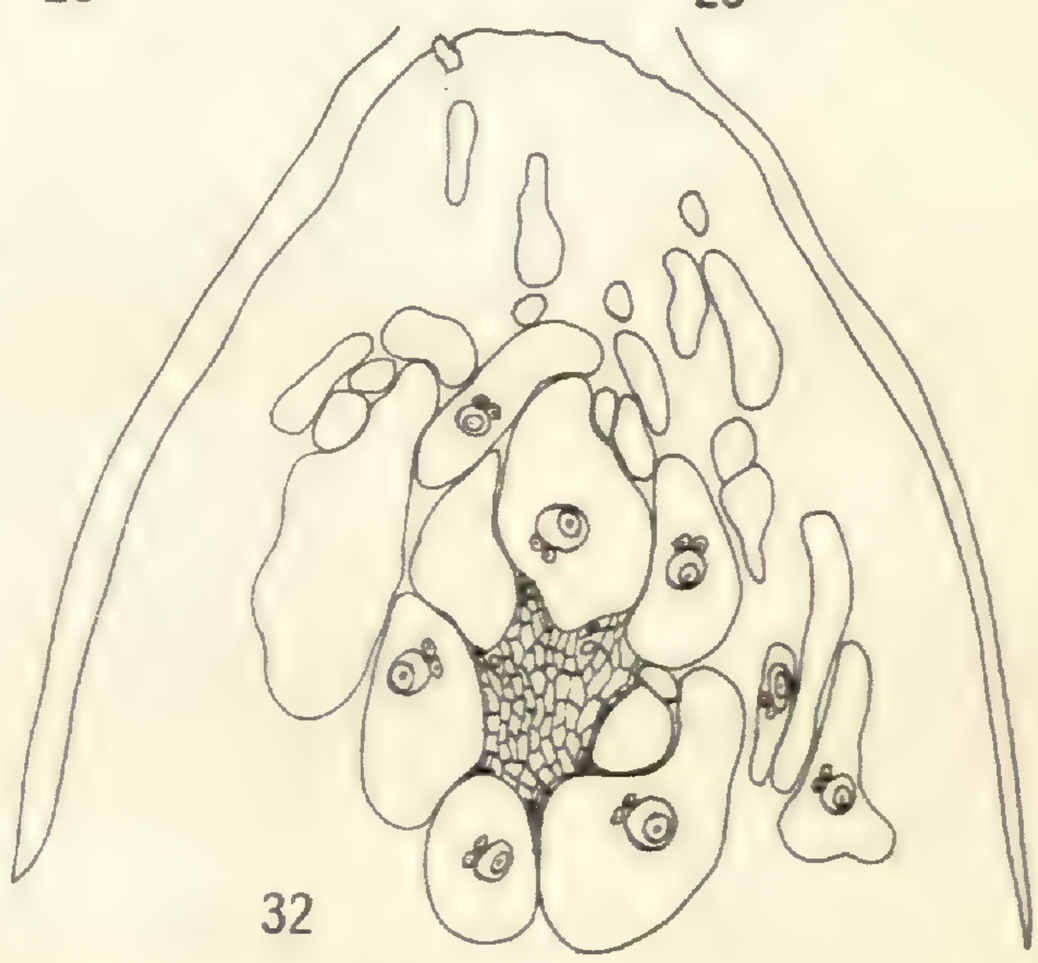
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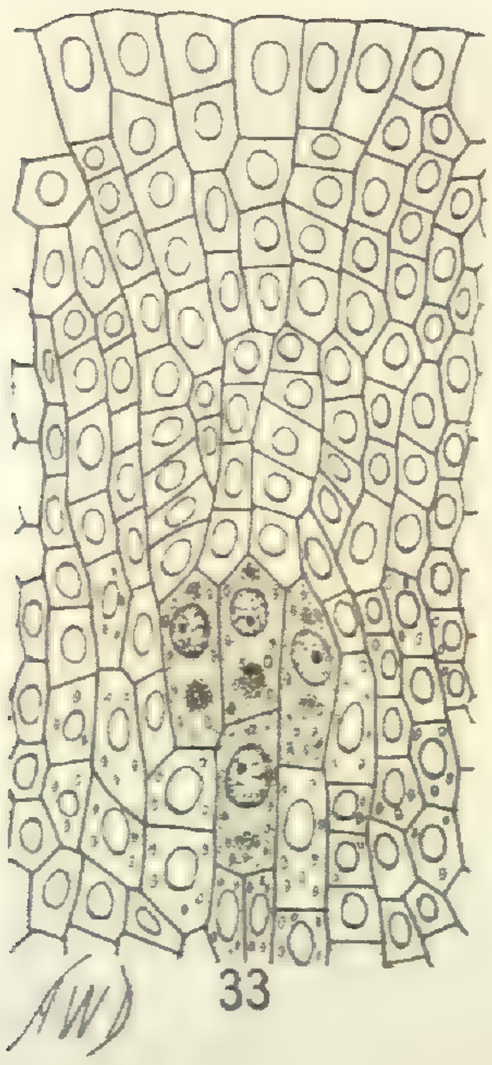
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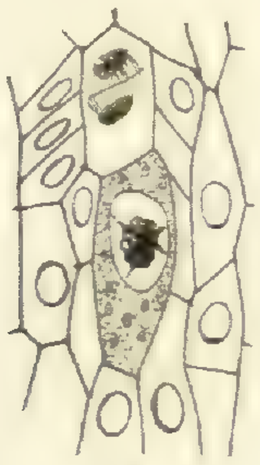
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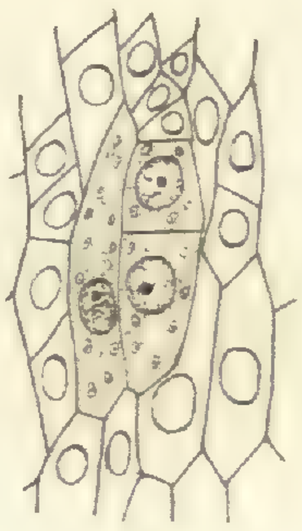
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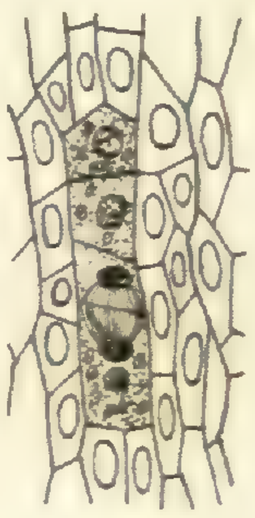
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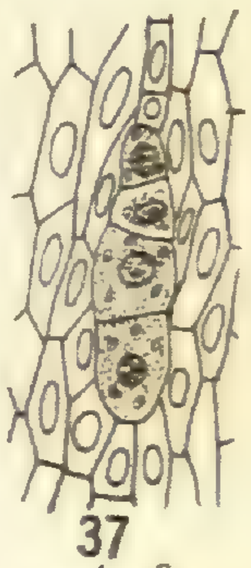
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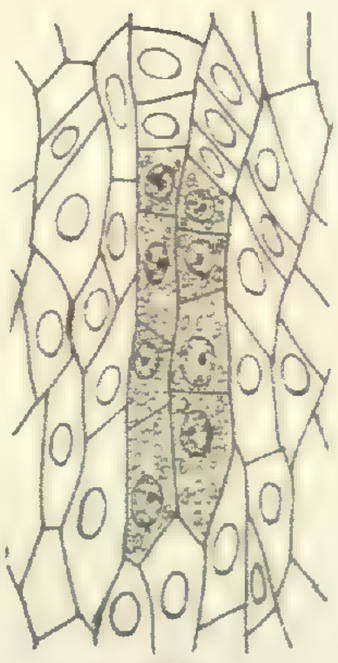
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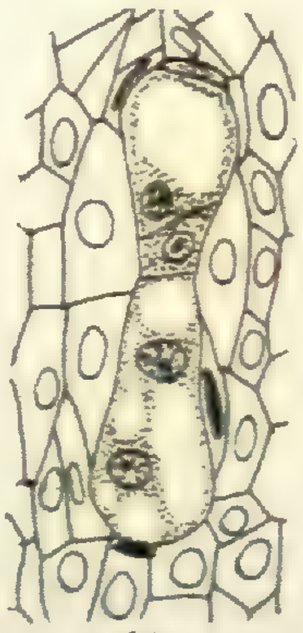
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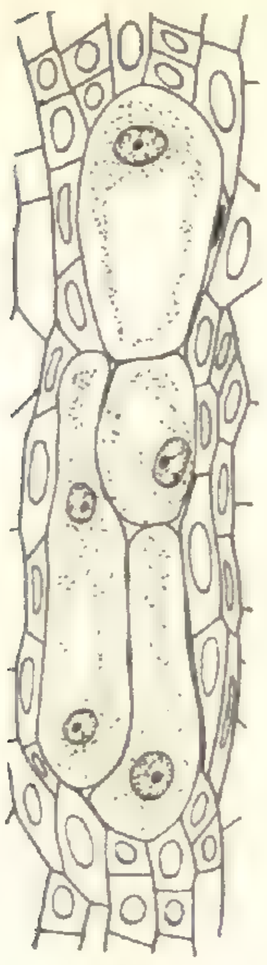

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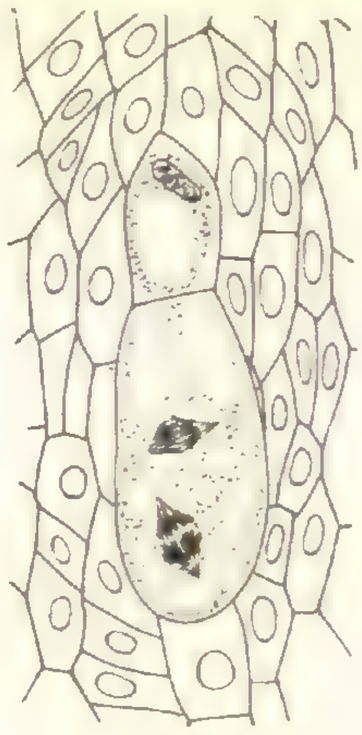

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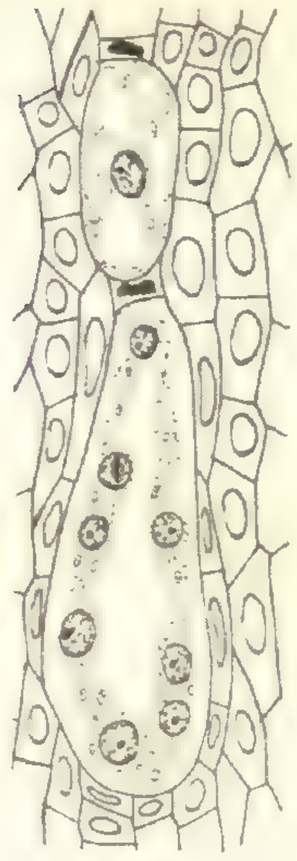

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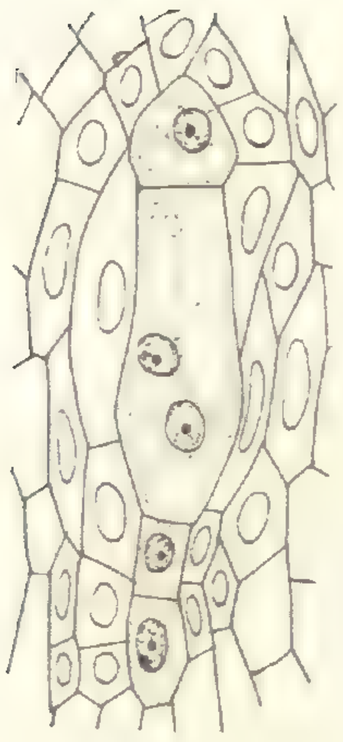

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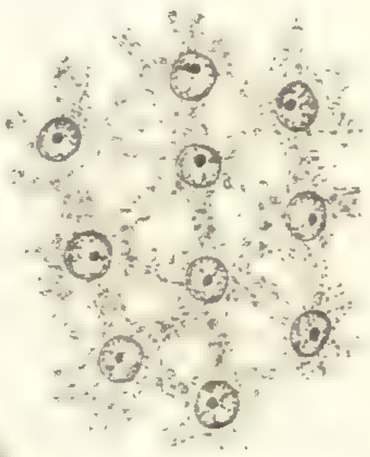

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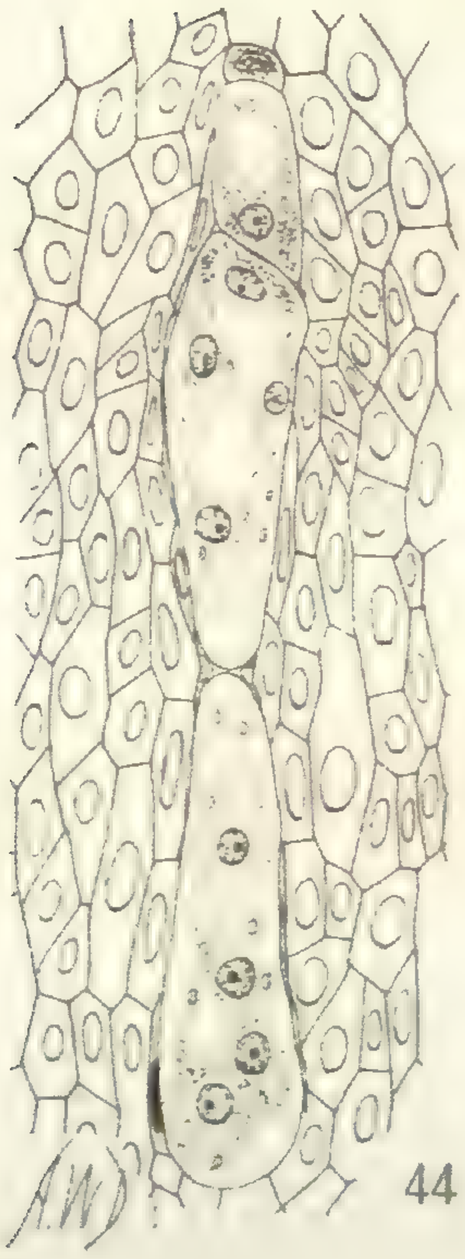

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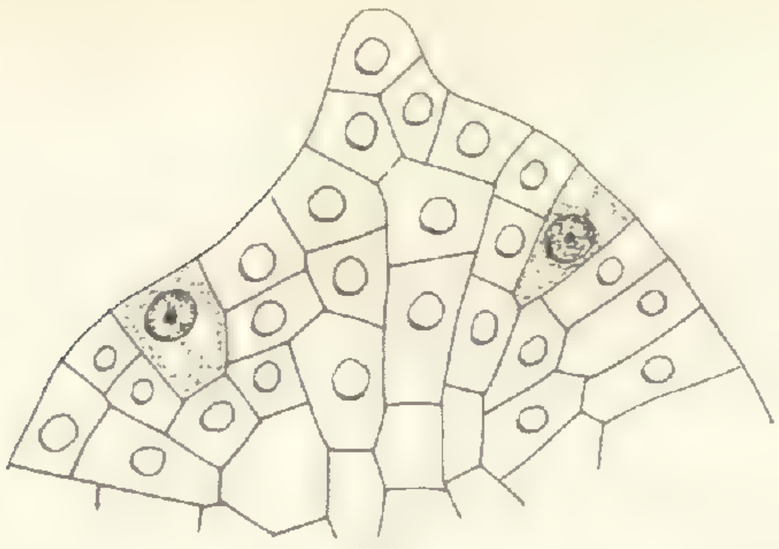

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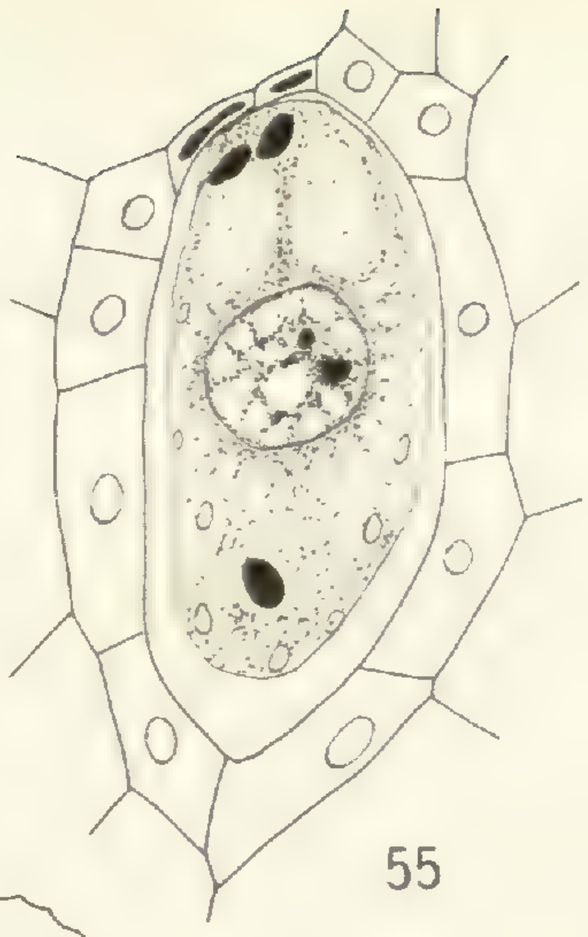

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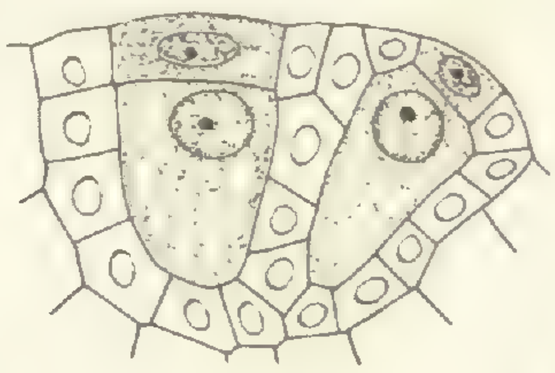

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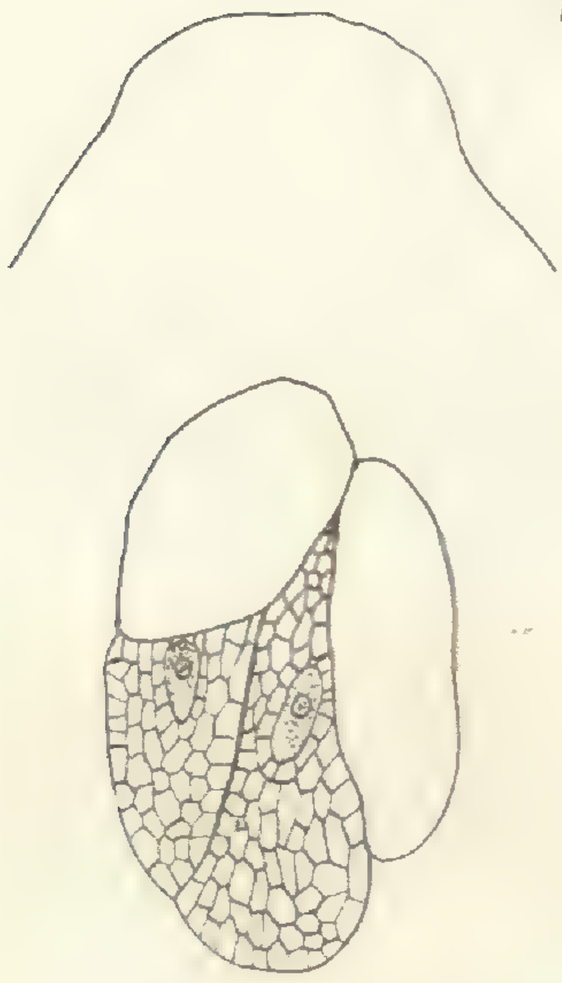

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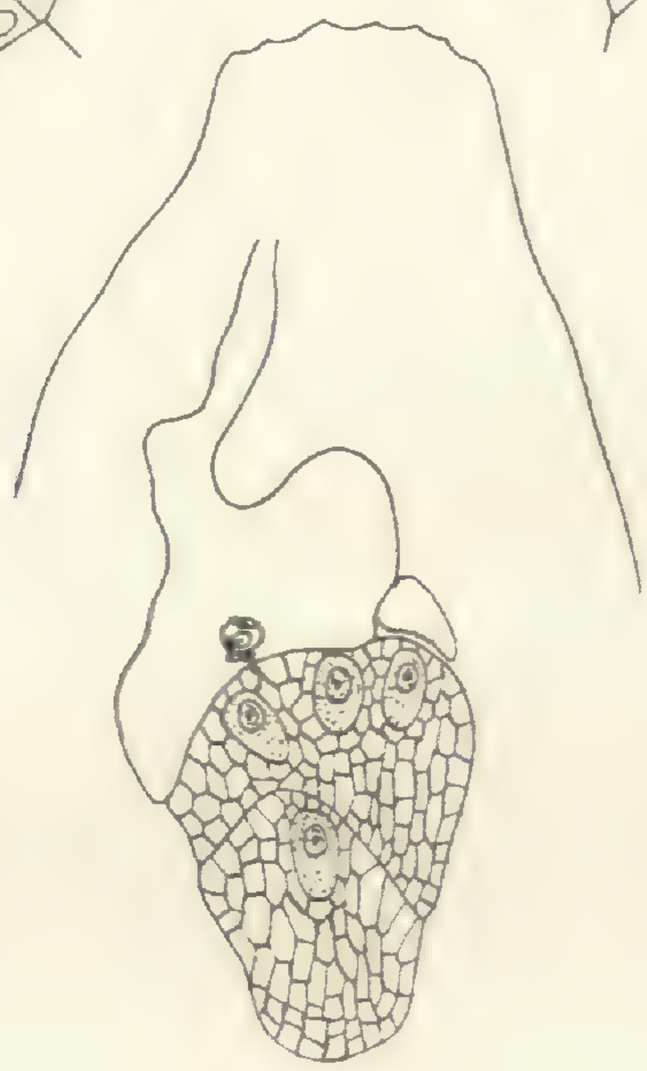

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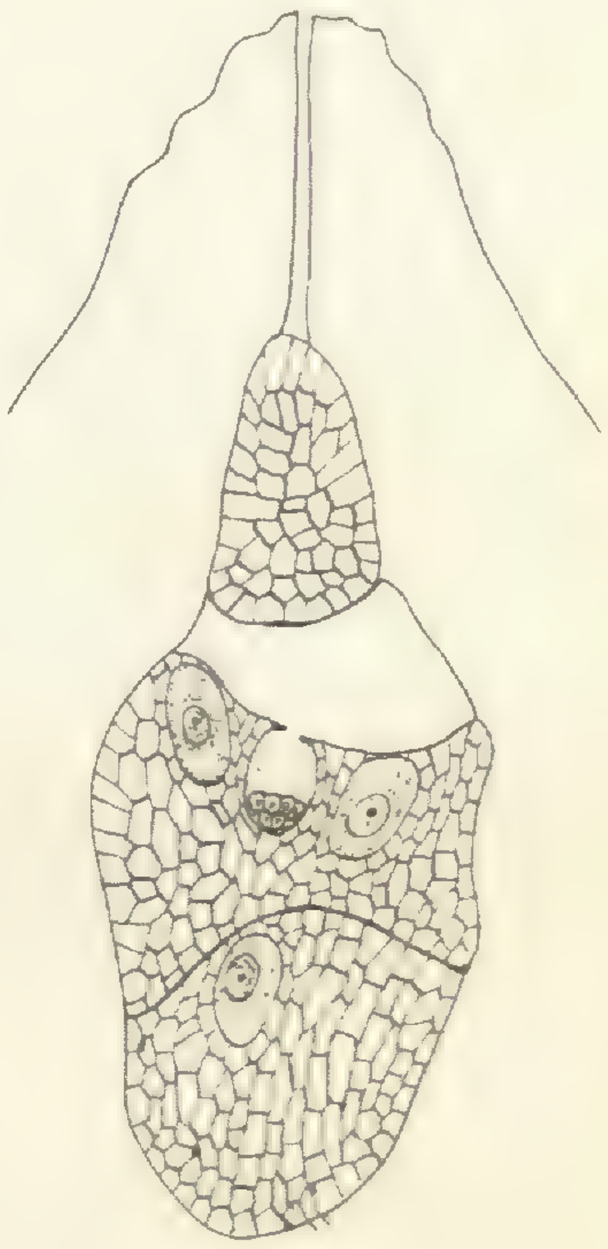

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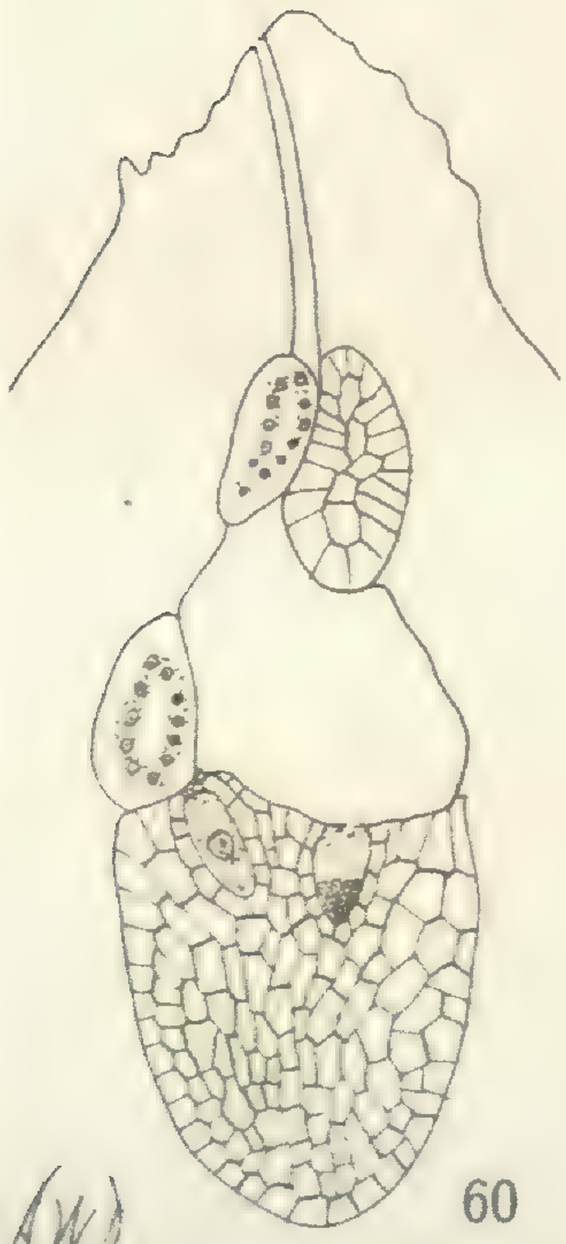

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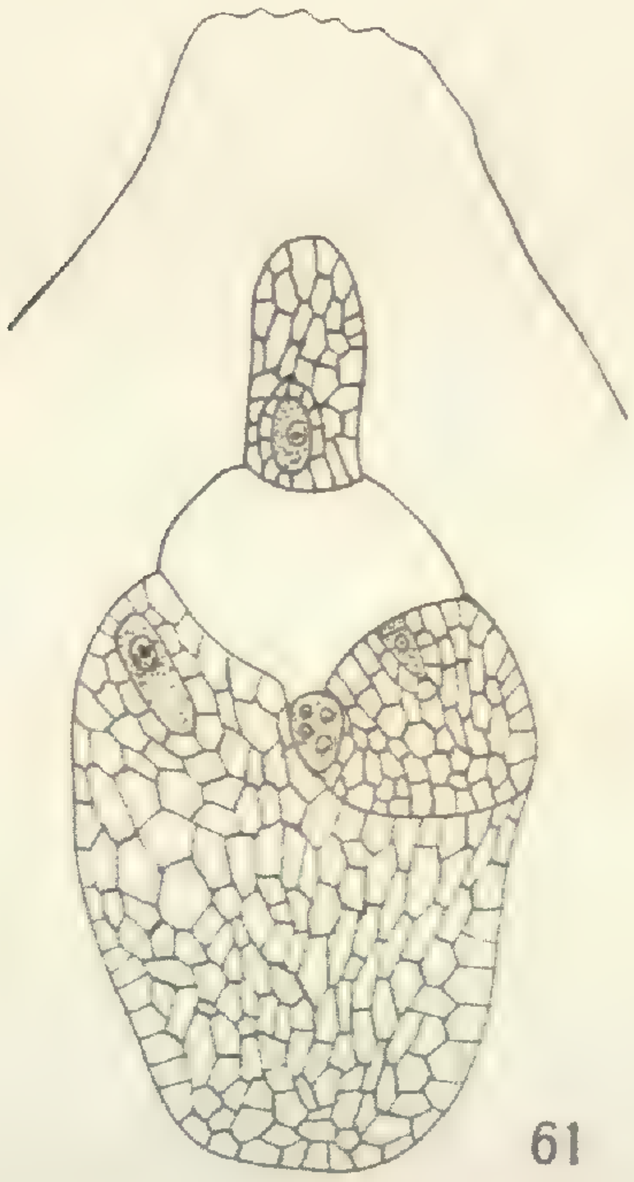

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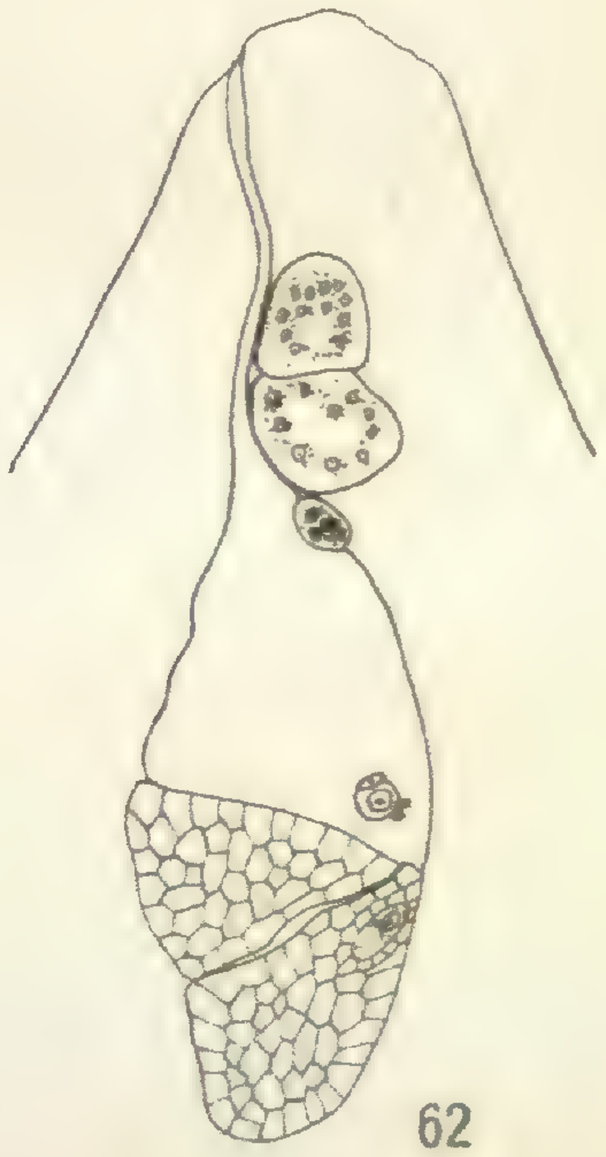


62

DUPLER on TAXUS

ARBORES FRUTICESQUE CHINENSES NOVI. IV

CAMILLO SCHNEIDER

(WITH PLATE XV)

Salix (sect. SCLEROPHYLLAE Schn.) **tenella,** n. sp. (fig. A, 1–6).—Frutex parvus squarrosus; ramuli hornotini non visi, annotini biennesque floriferi obscure purpurascentes, minute puberuli vel fere tomentelli, dein glabrescentes, vetustiores cinerascentes vel cinereo-brunnei. Folia nondum satis evoluta anguste elliptico-lanceolata, apice obtusa, basi subrotundata, 1–1.5 cm. longa, 0.2–0.4 cm. lata, superne viridia, initio plus minusve puberula, subtus discoloria, glaucescentia, sparse puberula vel ut videtur cito glabrescentia, nervis valde tenuibus utrinsecus circ. 6 superne incisis, margine integerrima; petioli 1–2 mm. longi, pilis subflavis tomentelli. Amenta tantum juvenilia feminea visa, coetanea, anguste cylindrica, 3–4 mm. crassa, ad 2.5 cm. longa, pedunculis folia 3–6 parva normalia gerentibus puberulis circ. 5 mm. longis exclusis, rhachi tomentella, densiflora; bracteae ovato-rotundae vel ovato-ellipticae, ovariis sublongiores, supra medium fuscae, apice subrotundatae, tantum versus basim laxe pilosae et paullo ciliatae, ceterum glabrae; ovaria sessilia, ovata, glabra vel partim sparse pilosa, stylo brevissimo ad basim bifido coronata; stigmata brevia, biloba; glandulae 2, ventralis late ovata vel ovato-rectangularis, dorsalis paullo minor, similis vel 2-partita.

Szechuan australis: in districtu Yen-yüan Hsien, prope pagum Liu-ku, ad vias, alt. circ. 3600 m., 18 Maji 1914, *C. Schneider* (no. 1304; typus in Herb. Arb. Arn. et Hb. Schneider; frutex parvus).

This species very much resembles some forms of sect. LONGIFLORAE Schn., but, according to the dorsal gland, it seems closely related to *S. atopantha* Schn., which may easily be distinguished by its hairy ovaries and bracts, and by the different shape of its ventral gland. The very young leaves of *S. tenella* show no distinct sign of a dentation.

Salix (sect. ERIOSTACHYAE Schn.) **Balfouriana,** n. sp. (fig. B, 1–4).—Arbuscula erecta, pulchra, ad 6 m. alta; ramuli annotini

subdense albo-villosuli, deinde fuscescentes vel nigrescentes, glabrescentes vel subglabri; gemmae juveniles dense villosae. Folia satis magna, late elliptica vel elliptico-oblonga, apice subito breviter acuta, basi rotundata, rarius leviter subcordata, minora inferiora 6–8 cm. longa, 2–3 cm. lata, majora superiora 9–12 cm. longa et 3.3–4.8 cm. lata, superne saturate viridia, adulta laxe (in costa densius) sericeo-villosula, subtus valde discoloria, pulcherrime albescentia, pruinosa (non papillosa), plus minusve (initio probabiliter dense) adpresse albo-sericeo-villosula, costa nervisque lateralibus utrinsecus circ. 8–12 angulo 50–80° a costa divergentibus flavescentibus utroque latere prominentibus, reticulo nervillorum gracillimo prominulo, margine integerrima; petioli 6–15 mm. longi, undique dense villosi, superne late sulcati; stipulae ut videtur minimae, indistinctae. Amenta tantum fructifera visa, tardiva, ramulos foliatos 1.5–4 cm. longos terminantia, cylindrica, ad 8 cm. longa et 1 cm. crassa, axi dense villosula. Flores adulti inter fructus remanentes circ. 6 mm. longi; ovaria ovato-oblonga, sessilia, dense albo-villosula; styli distincti circ. $\frac{1}{4}$ ovarii aequantes, ad basim bifidi, stigmatibus satis marcidis angustis oblongis bifidis brachiis styli fere aequilongis; glandula 1, ventralis, sicca ovato-trangularis, brevis; bracteae late ellipticae, apice rotundatae, pallidae vel brunnescentes utrinque villosae, ovario subtriplo breviores. Fructus maturi circ. 7 mm. longi, ovariis adultis similes, aperti valvis paullo recurvis.

Yunnan boreali-occidentalis: ad latera orientalia montium niveorum prope Lichiang-fu, in dumetis in valle magna infra glaciem magnam, alt. circ. 3400 m., 30 Julii 1914, *C. Schneider* (no. 2059; typus in Herb. Arb. Arn. et Hb. Schneider; arbuscula ad 6-metralis).

Unfortunately I collected only a few remnants of fruiting catkins, and I have seen neither young female flowers nor the male plant, but the leaves are so distinct that there can be no doubt that this willow represents an excellent new species. So far as I can judge by the material before me, it belongs to sect. ERIOSTACHYAE Schn., but it may be distinguished at once from all the other species by the beautiful snowy white under surface of its leaves.

To this species may also belong a sterile specimen collected by me in Szechuan australi, inter Hoh-si et Te-li-pu, alt. circ. 2000 m., 7 Maji 1914 (no. 1124; arbor parva ad 5-metralis). It differs from the type in having somewhat narrower ovate-oblong leaves which are much more acute at the apex, the larger ones measuring up to 9 cm. in length and up to 3 cm. in width.

The name is given in honor of Professor BAYLEY BALFOUR, the distinguished Scotch botanist and director of the Royal Botanic Garden at Edinburgh, which contains an extremely rich collection of living woody and herbaceous plants from China, especially from northwestern Yunnan.

Salix (sect. PSILOSTIGMATAE Schn.) **Guebriantiana,** n. sp. (fig. C, 1–5).—Frutex erectus, satis elongato-ramosus, ad 6 m. altus; ramuli novelli initio parce sericei, annotini biennesque glabri, rubro-fusci vel sordide brunnei; gemmae flavo-rubrae, oblongae, subglabrae. Folia juvenilia ovato-oblonga vel late lanceolata, apice sensim subacuminata, basi cuneata vel rotundata, 3–5 cm. longa et 1–1.5 cm. lata, superne initio sericea vel sericeo-villosa, cito subglabra, intense viridia, subtus plus minusve dense sericeo-villosa, dein glabrescentia, discoloria, pruinosa, nervis lateralibus utrinsecus circ. 12 angulo acuto a costa divergentibus, margine integerrima vel saepissime versus apicem dense minute glanduloso-serrata, matura ignota; petioli vix 5 mm. longi, laxe sericei; stipulae distinctae non visae. Amenta (mascula tantum visa) coetanea, anguste cylindrica, nondum satis evoluta ad 6.5 cm. longa et vix 7 mm. crassa, pedunculo ad 1 cm. longo folia 3–4 normalibus minora sed similia gerente excluso, axi laxe villosa; bracteae concolores pallidae vel apice leviter brunnescentes, obovato-orbiculariae, apice plus minusve truncatae et saepe leviter crenulatae, basi dorso leviter saccatae, glabrae, filamentis subduplo vel fere 3plo breviores, quam glandula dorsalis subduplo longiores; filamenta glabra, juvenilia satis crassa; antherae flavae, ovato-globosae; glandulae 2, separatae, ventralis lata, subquadrato-rotundata vel rectangularis et apice truncata, dorsalis illae vix vel paullo brevior sed angustior, oblonga, apice truncata.

Szechuan australis: inter urbem Yen-yüan Hsien et viculum Hun-ka, in dumetis collinis, 11 Junii 1914, *C. Schneider* (no. 1488; typus in Herb. Arb. Arn. et Hb. Schneider; frutex erectus vel arbuscula ad 6-metralis).

In its long narrow catkins this species very much resembles *S. phanera* Schn. and its relatives, but it may be distinguished from them at once by its glabrous bracts and filaments, as well as by the different shape of its broad ventral gland. The male flowers are not unlike those of *S. magnifica* Hemsl., which otherwise is extremely different. Unfortunately there are neither mature leaves nor female flowers, and without having seen those the relationship of this well marked species remains doubtful.

I take great pleasure in associating with this interesting willow the name of Mgr. DE GUÉBRIANT, bishop of the famous French Catholic Mission at Ning-yüan-fu, in appreciation of valued service rendered to me while I was staying in that town during the month of April 1914.

Salix (sect. PSILOSTIGMATAE Schn.) **wolohoensis,** n. sp. (fig. D, 1–5).—Frutex erectus, squarrosus, ad 2 m. altus; ramuli, novelli tomentosuli, dein glabrescentes, olivaceo-brunnescentes, biennes glabri, fuscescentes; gemmae foliiferae ovatae, obtusae, adpressae, breviter pilosae, flavobrunneae, circ. 4 mm. longae. Folia firma, etiam majora vix satis evoluta, late lanceolata vel anguste elliptico-lanceolata, apice sensim acuta vel minora subobtusa, basi late cuneata vel rotundata, minimis exceptis inferiora 3–4 cm. longa et 1–1.5 cm. lata, superiora ad 7 cm. longa et 2 cm. lata, superne sordide viridia, initio densius dein laxe adpresse sericeo-villosa, costa flavescente plana, nervis lateralibus subincisis, subtus valde discoloria, initio tomento sericeo subflavescente dense tecta, dein argenteo-cinerea, adpresse sericeo-villosa (pilis costae parallelibus), costa nervisque lateralibus circ. 8–10 angulo 45–60° a costa divergentibus flavescentibus prominulis, rete nervillorum haud vel indistincte prominulo, margine integerrima vel obscure minutissime distanter glanduloso-denticulata; petioli 2–4 mm. longi, superne sulcati, tomentosuli; stipulae minimae 2–3.5 mm. longae, semicordatae, glanduloso-denticulatae, ut folia pilosae. Amenta tantum fructifera visa, subsessilia, pleraque delapsa, ad 4 cm. longa et ad 8 mm. crassa, patentia, ad axim villosula, basi foliolis paucis parvis vix ad 1 cm. longis deciduis ceterum normalibus satis similibus instructa; flores inter fructus remanentes circ. 3 mm. longi; ovaria ovata, dense sericeo-villosula, sessilia; styli breves integri, stigmatibus iis aequilongis oblongis bifidis; glandula 1, ventralis, ovario 3-plo brevior, oblongo-rectangularis, apice truncata vel retusa (an juvenilis longior?); bracteae late obovato-orbiculares, apice subretusae, ovario subduplo breviores, distincte brunnescentes, intus subglabrae, extus laxe sericeo-villosae, margine praecipue apice pilis albis sericeis satis brevibus fere comoso-ciliatae. Fructus circ. 5 mm. longi, ovati, satis obtusi, aperti valvis strictis, bracteis quam in flore glabrioribus brevioribus, ceterum ut ovaria superne descripta.

Szechuan australis: inter oppida Yen-yüan Hsien et Yung-ning, in dumetis inter pagos Wo-lo-ho et Hu-ma-ti, alt. circ. 2000–2400 m., 16 Junii, *C. Schneider* (no. 3490; typus in Herb. Arb. Arn. et Hb. Schneider; frutex squarrosus ad 2-metralis).

This species much resembles *S. psilostigma* And., which I only know from the good specimens collected by A. HENRY and G. FORREST in Yunnan and mentioned by me in the Pl. Wils. 3: 116. From those the new species may be distinguished by its leaves being a little more hairy on the upper surface and not so thickly covered with a silvery silky pubescence on the lower one, by its much more glabrous bracts which are not densely silky outwardly, and by its shorter, entire, not deeply cleft styles. The fruiting catkins seem to be shorter in *S. wolohensis*. Without having seen the male plant, it seems impossible to determine the real relationship of this species, which comes from a region that has never been explored before by botanical collectors.

Salix (probabiliter sect. DENTICULATAE Schn.) **caloneura,** n. sp. (fig. G, 1–6).—Frutex elatior, divaricatus; ramuli hornotini annotinique glabri, flavescentes vel olivacei, vetustiores rubro-brunnei, interdum ad gemmas adpressas puberuli. Folia elliptica, obovato-elliptica vel maxima late elliptico-oblonga, apice satis subito breviter acuta, basi obtusa vel subrotundata, interdum subcuneata, superne intense viridia, subtus valde discoloria, albescentia, sub microscopio plus minusve papillosa, costa nervisque flavescentibus utrinque prominulis, nervis lateralibus versus marginem currentibus approximatis circ. 3–4 pro 1 cm. conspicuis, rete nervillorum satis distincto, valde juvenilia subtus distincte sericea, mox glabrescentia, adultiora superne ad costam sparse vel vix puberula, subtus in costa pilis sparsis praedita vel glabra, margine integerrima vel saepissime indistincte crenulata, ima basi interdum glandulis indistinctis 2 instructa, minora inferiora 4–7 cm. longa, 2–3.5 cm. lata, maxima superiora ad 9:3.5 vel 10:3 cm. magna; petioli 0.5–1.5 cm. longi, superne in sulco pubescentes. Amenta tantum fructifera visa, densa, ad 7 cm. longa et 1 cm. crassa, axi glabrescente, pedunculo ad 1.5 cm. longo folia satis parva sed normalia 3–4 gerente suffulta. Flores feminei inter fructus remanentes glaberrimi; ovaria ovato-oblonga, pedicellis glandulam unam ventralem anguste rectangularem apice truncatam fere duplo vel vix superantibus, stylo satis distincto fere ad basim bifido stigmatibus parvis brevibus satis obtusis longiore; bracteae ut videtur ovato-ellipticae, glabrae, fuscescentes, pedicellum ovarii circ. ⅓

superantes. Fructus maturi circ. 6 mm. longi, ovato-elliptici, glabri, ut ovaria pedicellati, pedicello glandulam siccam fere duplo superante.

Szechuan australis: in districtu Hua-li ad flum. Yalung, in dumetis, alt. circ. 2800 m., 27 Maji 1914, *C. Schneider* (no. 1425; typus in Herb. Arn. Arb. et Hb. Schneider).

Judging by the fruiting material only, I believe this species is best placed in sect. DENTICULATAE Schn. near *S. denticulata* And., but it can be distinguished at once from this species by its much larger leaves. The yellowish nervation is very conspicuous on both surfaces of the leaves. I am not able to determine the real relationship of the new species, not having seen any male specimen.

Salix (probabiliter sect. PHYLICIFOLIAE Dum.) **squarrosa,** n. sp. (fig. E, 1–5).—Frutex erectus, squarrosus, breviter ramosus, ad 4 m. altus; ramuli hornotini non visi, annotini nigro-purpurascentes, glabri vel praesertim ad gemmas parce pilosiusculi, biennes sordide brunnescentes vel ut vetustiores nigro-cinerascentes; gemmae foliiferae elliptico-oblongae, acutae, subadpressae, circ. 1 cm. longae, flavo-brunneae, glabrae. Folia nondum evoluta vel minima, vix ad 1 cm. longa et 3 mm. lata, superne glabra, subtus dense longe sericea sed ut videtur cito glabrescentia, integerrima, nervis lateralibus vix visibilibus, matura ignota. Amenta praecocia, sessilia, patentia, ovato-elliptica, vel breviter cylindrica, 1.5–2.8 cm. longa, circ. 1 cm. crassa, dense albo-sericea, tantum feminea visa; bracteae ovatae, subacutae, ovaria florum superantes sed vix apicem styli attingentes, nigro-fuscae, utrinque longe sericeae; ovaria ovata, dense breviter sericea, breviter pedicellata, pedicello glandulam aequante vel sublongiore; styli fere glabri, distincti, elongati, dimidio ovarii aequilongi, stigmatibus oblongis apice haud vel paullo emarginatis stylo brevioribus coronati; glandula una, ventralis, oblongo-rectangularis, apice truncata. Fructus vix satis maturi pedicello stigmateque incluso circ. 6 mm. longi, ovato-elliptici, ut ovaria sericei, bracteas subduplo superantes.

Szechuan australis: in districtu Yen-yüan Hsien, inter viculos Ka-la-pa et Liu-ku, in silvis montanis, alt. circ. 3800 m., 16 Maji 1914, *C. Schneider* (no. 1246; typus in Herb. Arb. Arn. et Hb. Schneider; frutex squarrosus, circ. 4 m. altus).

This is the first willow from central China, I have seen, which apparently represents a species of sect. PHYLICIFOLIAE Dum. It is a much branched tall shrub with short spreading branchlets. The short, silky female aments are perfectly sessile. Without having seen mature leaves and male flowers, however, it is impossible to be sure of the real relationship of the species.

Salix (sect. DIPLODICTYAE Schn.) **Faxoniana,** n. sp. (fig. H, 1–5).—Frutex parvus, ramis prostratis radicantibus, ramulis ascendentibus, 0.2–0.3 m. altus; ramuli tantum novelli initio sericei, annotini glabri, flavo-brunnei, biennes vetustioresque obscure brunnescentes, deinde nigrescentes; gemmae elliptico-oblongae, subacutae, circ. 5 mm. longae, glabrae. Folia obovato-elliptica, elliptica vel elliptico-oblonga (vel minima ovato-elliptica), apice rotundata, obtusa vel breviter subacuta, basi late cuneata vel rotundata, 1.5:1 cm. ad 3.5:2–2.3 cm. vel angustiora ad 3:1.5 cm. magna, superne intense viridia, subnitidula, glabra, tantum in costa subimpressa vel plana versus basim pilis sparsis praedita, subtus valde discoloria, cinerascentia vel albescentia, pruinosa, in costa nervisque lateralibus prominulis utrinsecus 6–10 angulo 70–80° a costa divergentibus pilis sericeis sparsis instructa vel glabra (juvenilia probabiliter dense sericea), reticulo nervillorum satis distincto, margine satis indistincte et distanter glanduloso-crenato-denticulata; petioli satis longi, superne in sulco lato plus minusve puberuli, 8–13 mm. longi. Amenta tantum fructifera visa, ramulos ad 3 cm. longos normaliter foliatos terminantia, cylindrica, densiflora, ad 5 cm. longa et circ. 1 cm. crassa, axi laxe villosula; bracteae florum inter fructus remanentium oblongae, fuscae, obtusiusculae, dimidio ovarii aequantes, versus basim parce villosulae, apicem versus glabrae, plus minusve ciliatae; ovaria elongata, conica, basi in pedicellum brevissimum quam glandula duplo breviorem attenuata, glabra vel basi sparse villosula; styli distincti, ovariis junioribus $\frac{1}{3}$ vel subduplo breviores, fere ad medium fissi, brachiis divaricatis stigmatibus parvis brevibus bifidis coronatis; glandula una ventralis, oblonga, obtusa, pedicellum duplo superans. Fructus circ. 8 mm. longi, apice attenuati, aperti valvis recurvatis, glabri vel ima basi puberuli, bracteis et glandulis siccis ut in ovario minoribus.

Yunnan boreali-occidentalis: in rupestribus ad latera orientalia montium niveorum prope Lichiang-fu, alt. circ. 4000 m., mense Augusto 1914, *C.*

Schneider (no. 2319; typus in Herb. Arb. Arn. et Hb. Schneider; frutex 0.2–0.3 m. altus); in declivibus rupestribus montium inter flum. Yang-tze et oppidum Chung-tien, alt. circ. 3400 m., mense Augusto 1914, *C. Schneider* (no. 2375; forma nullo modo ab no. 2319 diversa).

At first sight this species very closely resembles *S. oreinoma* Schn. from the high mountains of western Szechuan, but *S. Faxoniana* differs from it and from the other Asiatic species of sect. DIPLODICTYAE Schn. in its glabrous ovaries, the fruits being sometimes hairy only at the very base. The leaves are similar to those of *S. oreinoma*, but the catkins of this species measure only about 2 cm. in length (without the peduncle), and the bracts are more glabrous, broader, and truncate at the apex. The species is named in compliment to MR. C. E. FAXON, the assistant director of the Arnold Arboretum.

SALIX BRACHISTA Schneider in Sargent, Pl. Wils. 3:145. 1916.—I described only a male specimen, and I add the following description of the female plant: Frutex pygmaeus, trunco subterraneo, ramis procumbentibus radicantibus; ramuli prostrati, initio olivacei vel flavescentes, dein flavo-brunnei vel flavo-rubri, tantum novelli parce pilosuli, cito glabrescentes. Folia parva vel perparva, crasse papyracea, elliptica vel ovato-elliptica, utrinque acuta vel pleraque apice acutiuscula et basi subrotundata, minimis exceptis 6:2 mm. ad 12:6 mm. vel maxima ad 17:9 mm. magna, superne satis viridia, costa incisa, nervis lateralibus planis vel vix levissime prominulis, glabra, subtus pallidiora, non glaucescentia, costa nervisque lateralibus utrinque 5–7 angulo circ. 50–70° á costa divergentibus distincte prominulis, an initio pilosa?, adulta glabra, margine subintegerrima vel plus minusve distanter minute denticulata; petioli glabri, superne sulcati, 2–4 vel foliorum maximorum ad 8 mm. longi, gemmas plus minusve duplo superantes. Amenta fructifera pauca tantum visa, ramulos breves normaliter paucifoliatos terminantia, 2–4-flora; fructus maturi, obovato-oblongi, apice attenuati, 6–7 mm. longi, glabri, brunnei, aperti valvibus apice recurvatis, subsessiles, pedicello glandula subbreviore; styli sicci breves, stigmatibus ut videtur brevibus coronati; glandula 1, ventralis, satis late rectangularis, pedicello sublongior; bracteae pallidae, glabrae, obovato-oblongae, apice retusae vel rotundatae, capsulis fere duplo breviores.

Yunnan boreali-occidentalis: ad latera orientalia montium niveorum prope Lichiang-fu, in rupestribus calcareis in valle infra glaciem magnam, alt. circ.

3500 m., mense Augusto 1914, *C. Schneider* (no. 3454; ramuli fructiferi in Herb. Schneider).

It is with some hesitation that I refer this female willow to *S. brachista* Schn., which is known only from male specimens collected by E. H. WILSON in western Szechuan. In most of my specimens there are no flowers or fruits, the apex of the branchlets being infected probably by an insect and transformed into hairy galls. The leaves agree well with those of typical *S. brachista* in the nervation and color.

Together with no. 3454, I collected another female willow (no. 2318), the leaves of which are even a little smaller, of a somewhat firmer texture, with veins slightly impressed above and scarcely visible on the rather bluish grey under surface. I am not sure whether or not this form belongs to the Himalayan *S. Lindleyana* Wall. or represents a form of *S. Souliei* Seemen. It is not quite identical with those female plants from Tachien-lu which I described in Pl. Wils. **3**:62 as *S. Souliei.* I think it best, therefore, to give the following description of no. 2318 from the snow mountains near Lichiang-fu:

Frutex pygmaeus facie *S. Lindleyanae* Wall. vel *S. serpyllifoliae* Scop. ramis solo vel rupestribus adpressis, ramulis brevibus junioribus olivaceis glabris (an novellis pilosiusculis?). Folia perparva, crassiuscula, elliptica vel ovato-elliptica, utrinque obtusa vel subacuta, rarius basi subrotunda, minimis exceptis 5–7 mm. longa, 2–3 mm. lata, superne satis laete viridia, glabra vel in costa incisa sparse pilosa, nervis lateralibus plus minusve distincte incisis, subtus satis discoloria, glaucescentia (etiam novella?), costa prominula, nervis lateralibus utrinsecus 2–4 angulo 40–45° a costa divergentibus vix vel haud visibilibus, margine integerrima vel saepius plus minusve minute denticulata; petioli distincti, 2–4 mm. longi, superne interdum pilosiusculi, gemmas duplo superantes. Amenta ramulos perbreves normaliter foliatos terminantia, fructifera subcapitata, circ. 5-flora, in axi sparse pilosa; flores adulti glaberrimi, circ. 4–4, 5 mm. longi; ovaria ovato-conica, apice attenuata, basi plus minusve pedicellata, pedicello glandula sublongiore vel subbreviore; styli breves sed distincti, ad medium bifidi, stigmatibus brevibus oblongis emarginatis bifidisve brachiis styli subaequilongis; glandula 1, ventralis, oblongo-rectangularis, apice truncata; bracteae flavescentes vel in sicco flavo-brunneae obovato-oblongae vel oblongo-ellipticae, apice rotundatae, retusae vel emarginatae, ovariis circ. $\frac{1}{3}$ breviores. Fructus maturi ovati, aperti valvibus apice paullo recurvis, ceterum ut ovaria (fig. F, 1–4).

Salix (? sect. SIEBOLDIANAE Seem.) **dibapha,** n. sp. (fig. I, 1–6).—Frutex erectus, ad 4 m. altus, ramuli hornotini laxe vel densius villosuli (novelli satis dense flavescenti-tomentelli), annotini satis glabrescentes, atro-fusci, vetustiores glabri; gemmae foliiferae ut videtur flavo-purpureae, subglabrae. Folia papyracea, elliptica vel elliptico-oblonga, apice acuta vel longiora sensim breviter acuminata, basi cuneata, superne vivide laete viridia, tantum valde juvenilia plus minusve flavescenti-sericeo-tomentella, costa prominula nervisque partim exceptis cito glabra, subtus valde discoloria, glauca, pruinosa, initio ut supra sericeo-tomentella, sed citissime glabrescentia, tantum in costa elevata parce sericea, nervis lateralibus utrinsecus 10–20 angulo 80–90° a costa divergentibus prominulis, reticulo nervillorum foliorum immaturorum valde tenui vel vix visibili adultorum probabiliter magis conspicuo, margine integerrima, minimis exceptis inferiora elliptica 4–6 cm. longa et 1. 4–2 cm. lata, superiora oblongiora ad 8 : 2 .4 cm. magna; petioli 4–7 mm. longi, undique sericeo-villosuli; stipulae minimae, semicordato-lanceolatae, villosulae, margine glanduliferae, vix ad 3 mm. longae. Amenta tantum fructifera visa, praecocia, elongato-cylindracea, pedunculo ad 1 cm. longo foliola pauca parva ad 1 .5 cm. longa ab normalibus vix diversa gerente excluso ad 8 cm. longa et 0 .9 cm. crassa, axi villosa; flores inter fructus remanentes 2–3 .5 mm. longi; ovaria ovata, sessilia, dense villosula; styli breves sed distincti, $\frac{1}{4}$–$\frac{1}{5}$ ovarii aequantes, apice breviter bifidi, stigmatibus brevibus subbifidis oblongis; glandula 1, ventralis, oblonga, satis brevis, bracteis florum adultiorum subduplo brevior; bracteae ovariis juvenilioribus aequilongae, elliptico-oblongae, obtusae, brunnescentes, intus glabrae, extus infra medium villosulae et ciliatae, apice glabrae, ovariis adultioribus fere 3-plo breviores. Fructus subsessiles, ovato-oblongi, apice paullo attenuati, basi in pedicellum glandula breviorem contracti, satis dense albido-villosuli, stylis siccis exceptis circ. 3 .5–4 mm. longi, aperti valvis apice paullo recurvis.

Yunnan boreali-occidentalis: inter oppida Yung-ning et Yung-peh-ting, in pratis ad ripas prope viculum Pi ji, 24 Junii 1914, *C. Schneider* (no. 1646; typus in Herb. Arb. Arn. et Herb. Schneider; frutex ad 4-metralis).

Without having seen male flowers, it is difficult to judge the relationship of this species. It mostly resembles *S. hylonoma* Schn., which may be chiefly

distinguished by its more acuminate leaves with a longer silky pubescence on the under surface, by its somewhat thinner fruiting catkins, its longer gland, and by its longer more deeply cleft styles. The specific name is derived from δίβαφος, "double colored."

In Pl. Wils. 3:122 I described a *S. isochroma*, referring it to sect. HETEROCHROMAE Schn., but according to further observations I believe that this species represents only a variety of *S. hylonoma;* therefore, I suggest the following combination: S. HYLONOMA var. **isochroma** Schn., n. var.

Alnus (subgenus CREMASTOGYNE [Winkl.] Schn.) **Ferdinandi-Coburgii,** n. sp.—Arbor; ramuli novelli ut videtur dense fulvo-villosulo-tomentelli, annotini plus minusve glabrescentes, atrofusci, lenticellis sparsis flavo-brunnescentibus obtecti, vetustiores nigrescentes; gemmae stipitatae, subglobosae, subglabrae, resinosae. Folia matura chartacea, late elliptica vel subobovato-elliptica, apice satis subito in acuminem brevem producta, basi rotundata vel fere semper cordata, minora 5–7.5 cm. longa, 2.5–4 cm. lata, maxima ad 14:8 cm. magna, margine praesertim ad apicem satis distanter aequaliter breviter glanduloso-denticulato-serrata, superne satis obscure viridia, costa incisa breviter glanduloso-pilosa excepta glabra, nervibus planis, subtus discoloria, glaucescentia, pruinosa et sub microscopio subpapillosa, glandulifera, ad costam nervosque laterales valde prominentes flavobrunneos utrinsecus 12–17 plus minusve fulvo- (et glanduloso-) villosula (novella probabiliter satis dense tomentella) vel fere omnino glabrescentia; petioli crassi, superne sulcati, glanduloso-villosuli, 6–12 mm. longi. Amenta tantum feminea fructifera visa, pro subgenere *Cremastogyne* normalia, ovato-elliptica vel ovato-subglobosa, ad 2 cm. longa et 1.5 cm. crassa, plus minusve resinosa; pedunculi 10–15 mm. longi, laxe villosuli; bracteae ut in tabula fig. K, 2–4 delineatae, apice breviter obtuse lobatae et incurvatae, fere glabrae sed resinosae, circ. 12 mm. longae et (apice) subaequi latae; semina obovato-rectangularia, circ. 4 mm. longa, alis angustissimis cincta.

Yunnan boreali-occidentalis: in montibus Tsang prope Tali-fu, in vallibus ad latera orientalia, alt. circ. 2800 m., 3 Octobris 1914, *C. Schneider* (no. 2716; typus in Herb. Arb. Arn. et Hb. Schneider).

This interesting alder certainly belongs to sect. CREMASTOGYNE Winkler, which I raised to the rank of a subgenus in Pl. Wils. 2:492. 1916. In many respects it resembles *A. lanata* Duthie, but it may be distinguished from it, as well as from *A. cremastogyne* Burk., by the much shorter peduncle of its fruits, and especially by the almost wingless seeds which are entirely different from

the broadly winged seeds of the two other known species of this group. The male and female flowers of the new species are yet unknown.

As I pointed out (l. c.), the subgenus *Cremastogyne* is a very distinct one, and differs widely from subg. *Alnus* Endl. and *Alnaster* Endl. in its single male and female aments, which appear in the spring on this year's branchlets in the axils of normal leaves. The male flowers are entirely apetalous (fig. K, 6–9), and the female flowers, so far as I can see, agree well with those of the other subgenera; they are shown in fig. K, 10–12. In fig. K, 12, the small "prophylla" of the female flowers can be seen, which are hairy at the apex. In *A. cremastogyne* the female flowers I have seen had always 3 stigmas. The fruiting bracts and the seeds of *A. lanata* are represented in fig. K, 14–16; those of *A. cremastogyne* are very similar.

I take the liberty of dedicating this excellent species to His Majesty King Ferdinand I of the Bulgarians, an eminent botanist and patron of natural history.

ARNOLD ARBORETUM

EXPLANATION OF PLATE XV

FIG. A.—*Salix tenella:* *1*, young female flower with bract; *2*, *3*, stigmas; *4*, ventral gland; *5*, dorsal gland; *6*, bract with dorsal gland.

FIG. B.—*Salix Balfouriana:* *1*, old female flower with bract; *2*, ventral gland; *3*, bract; *4*, mature fruit.

FIG. C.—*Salix Guebriantiana:* *1*, young male flower; *2*, anthers; *3*, ventral gland; *4*, both glands with the base of the filaments between them; *5*, bract with dorsal gland.

FIG. D.—*Salix wolohoensis:* *1*, old female flower with bract; *2*, stigmas; *3*, ventral gland; *4*, bract; *5*, ripe fruit.

FIG. E.—*Salix squarrosa:* *1*, female flower with bract; *2*, stigmas; *3*, *4*, ventral gland and pedicel of the ovary; *5*, bract.

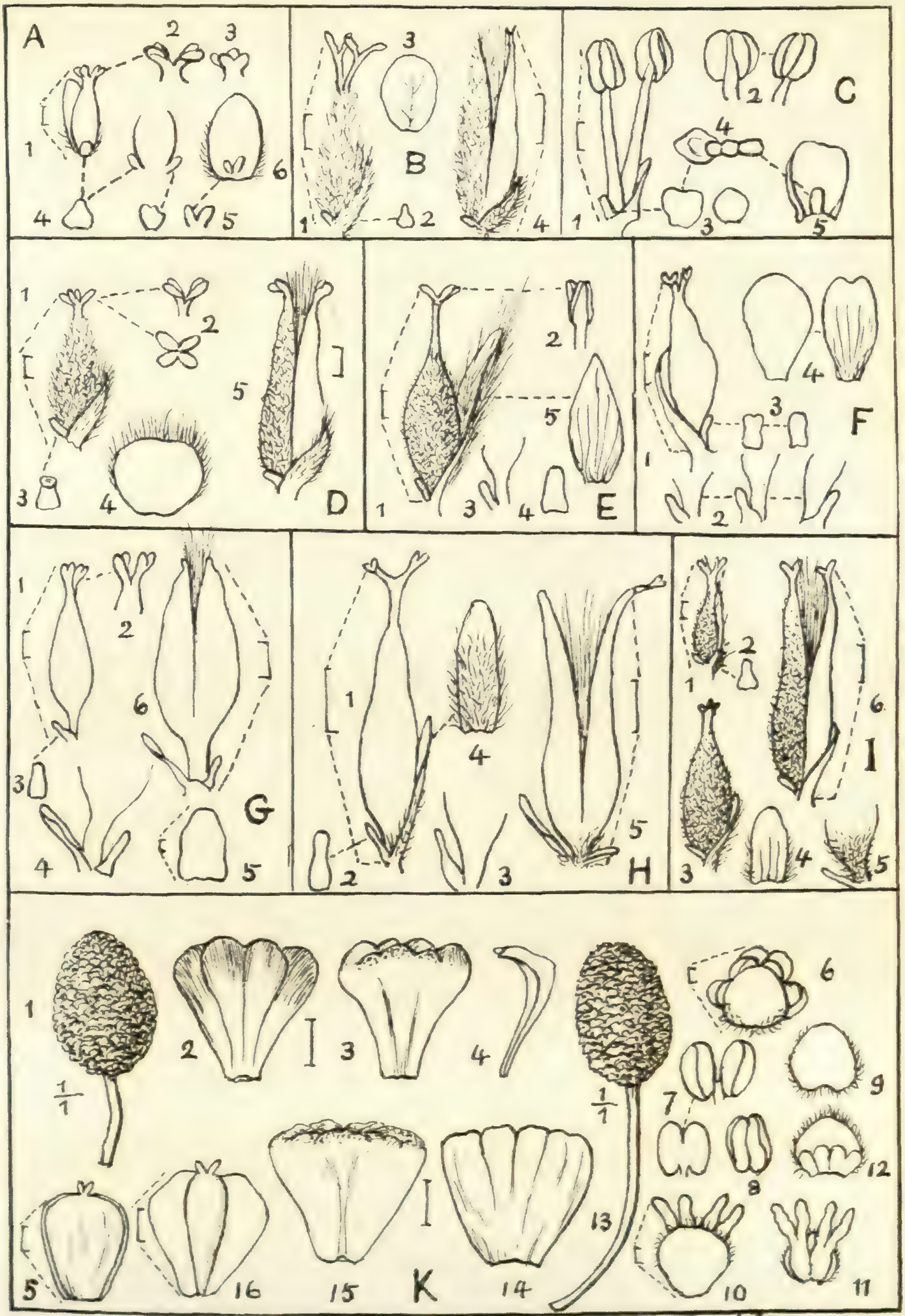
FIG. F.—? *Salix Lindleyana:* *1*, female flower with bract; *2*, ventral gland and pedicel of the ovary; *3*, ventral gland; *4*, bract.

FIG. G.—*Salix caloneura:* *1*, female flower; *2*, stigmas; *3*, ventral gland; *4*, pedicel of the ovary with bract and gland; *5*, bract; *6*, fruit.

FIG. H.—*Salix Faxoniana:* *1*, female flower; *2*, ventral gland; *3*, gland and pedicel of the ovary; *4*, bract; *5*, ripe fruit.

FIG. I.—*Salix dibapha:* *1*, young arrested female flower; *2*, its ventral gland; *3*, older female flower; *4*, bract; *5*, base of the ovary and gland; *6*, ripe fruit.

FIG. K.—*1–5*, *Alnus Ferdinandi-Coburgii:* *1*, ripe strobile; *2*, fruiting bract ventral; *3*, same dorsal; *4*, same lateral; *5*, seed: *6–16*, *Alnus lanata;* *6*, male dichasium with bract (front view); *7*, male flower; *8*, anther; *9*, bract; *10*, *11*, female dichasium with bract; *12*, bract with flowers removed showing their "prophylla"; *13*, ripe strobile; *14*, fruiting bract ventral; *15*, same dorsal; *16*, seed.



SCHNEIDER on CHINESE PLANTS

REPRODUCTION IN THE CONIFEROUS FORESTS OF NORTHERN NEW ENGLAND[1]

BARRINGTON MOORE

This investigation was undertaken to determine the factors governing the reproduction of the more important coniferous trees in the forests of northern New England. A detailed study of a single area was considered more effective than general observations over a wide area, but the study is not by any means exhaustive for the single area.

The work was done on Mount Desert Island, situated toward the eastern end of the coast of Maine, in about the same latitude as the northern part of the Adirondacks and northern New Hampshire. The island is included in the spruce region according to HAWLEY and HAWES (3). This is strictly correct; nevertheless, parts of the island show unmistakable signs of the more southerly white pine region. The location of the island is therefore of unusual interest. Being at the edge of the tension zone between two important regions, each with a distinct flora, there is a good opportunity to determine whether or not the northward migration of plants is still going on, and, if so, to study not only the rate of this migration, but also the many intricate factors involved in this phenomenon. Fortunately, about 5000 acres of this island have been made into a National Park, not only for purposes of recreation, but for scientific research in plant and animal ecology and in forestry.

The island is roughly 12 miles long by 15 miles wide, with a granite core running about northeast and southwest through its southern half. This granite has been cut across by glacial and water action in 9 places, so that instead of a continuous ridge we have a series of small mountains, 7 of them rising to over 1000 ft. above the sea. The northern slopes are gentle, the southern slopes

[1] Delivered at the New York meeting of the Ecological Society of America, December 28, 1916.

are precipitous, due probably to water action during the post-glacial submergence (5). The northern half of the island is comparatively level. The topography therefore offers a diversity of habitats.

The climate of the island is a curious mixture of the marine and the inland, the former, of course, predominating, but the latter being found in places shut off from the ocean winds. On the northeast side of the island the average annual precipitation is 48.3 inches, of which 16.1 inches or one-third comes in the growing season (May–September inclusive). This should be abundant, but there are periods during the summer in which lack of moisture is an important factor.

The mean annual temperature is 44° F., running from 21° in January to 65.5° in July. The sea tends to keep the temperature uniform, but it is uniformly cold, for it is beyond the Gulf Stream. There are surprising fluctuations in temperature, however. The large areas of exposed granite rock take up and radiate great quantities of heat, so that the fluctuations, particularly in places cut off from the ocean winds, must have a distinct bearing on the vegetation.

The vegetation, although predominantly northern, contains a strong mixture of middle Atlantic elements. It contains not only plants but forest associations belonging to both the boreal and the transition zones (4). Furthermore, this island and Schoodic Point, a small peninsula about 10 miles to the eastward, are isolated stations for *Pinus divaricata*.

The forest associations of the island are 5 in number: (1) spruce, (2) white pine, (3) cedar, (4) pitch pine, (5) grey birch-aspen. Over most of the island, except the parts recently burned, the first 3 associations mingle in a rather confusing manner to form a forest containing varying proportions of red spruce, balsam fir, white pine, and white cedar, with an admixture of red maple, grey birch (giving place to paper birch and yellow birch on the cooler, moister sites), aspen, and occasionally red oak.

1. The spruce association is composed of nearly pure spruce, (*Picea rubens*), mixed with hemlock (*Tsuga canadensis*), balsam fir (*Abies balsamea*), white cedar (*Thuja occidentalis*), and white pine

(*Pinus Strobus*). It occurs on almost any site, even bare rock, provided there is moisture.

2. The white pine association, composed of nearly pure white pine, is not abundant. The association on Mount Desert, although predominantly white pine, contains a strong admixture of red spruce and cedar, and sometimes of red pine (*Pinus resinosa*). It occurs on somewhat drier sites than the spruce association.

3. The cedar association does not form as pure stands as the two preceding ones. Although cedar predominates numerically, there are generally considerable proportions of fir, spruce, and white pine, with red maple (*Acer rubrum*) and paper birch (*Betula papyrifera*). It occupies the moist flats.

4. The pitch pine (*Pinus rigida*) association, generally sharply separated from all others, is composed of pure pitch pine, or sometimes pitch pine and a little red pine. It occupies mostly the dry rocky southern exposures. On rocky flats not exposed to full isolation, white pine, fir, and spruce are creeping in under the pitch pine; on these flats, if not elsewhere, the pitch pine appears to be a pioneer association.

5. The grey birch-aspen (*Betula populifolia–Populus tremuloides* and *P. grandidentata*) association is temporary, following fires, and is replaced sooner or later by the original coniferous forest.

A striking feature of these forests, a feature common to many spruce forests in the west as well as in the east, is the preponderance of fir reproduction under the spruce, even when the parent stand is nearly pure spruce. It is unnecessary to go into the many hypotheses advanced to explain this. Perhaps the most widespread theory, and the one tried out in this investigation, is that the accumulation of acid in the soil under the spruce is detrimental to spruce and favorable to fir. COVILLE's work on the blueberry (2) shows that certain plants do require acidity in the soil. Could it be that fir is one of those plants, and that spruce, though tolerant of acid, is not positively benefited by it as the fir appears to be? To determine this point, seedlings of red spruce, balsam fir, and white pine were transplanted from the forest into 3 different kinds of soil. The shoots of these seedlings were measured every 5 days for growth in length. The seedlings were of approximately the

same size and age, and were taken from the same place, so that variations due to size and vigor are eliminated. Each soil was placed in a flat approximately 8 cm. in depth, over which was placed a lath screen made so as to give half shade. All flats were in the open, were given no artificial watering after the first 2 days, and consequently were all under the same conditions except for the soil. These conditions were, furthermore, as close to natural forest conditions as possible.

The 3 soils were (1) A thoroughly decomposed forest humus which had been taken from the forest and rotted in a field for 2 years. This has a moisture-holding capacity, when saturated, of 138.5 per cent of its air-dry weight, or 82.6 per cent of its volume. (2) Undecomposed raw humus, taken directly from the spruce association, consisting of needles, cone scales, and other forest litter. This is COVILLE's "upland peat," the forest "duff" which accumulates in northern regions because decomposition is retarded by lack of sufficient warmth. Its moisture-holding capacity, saturated, is 504.6 per cent of its air-dry weight, but only 65.1 per cent of its volume. The high percentage of water on the basis of air-dry weight gives an idea of the extreme lightness of this raw humus. (3) Mineral soil from beneath the raw humus. This is a bouldery glacial till, a reddish brown sandy loam with but little clay (practically nothing remains in suspension after about an hour and a half). The moisture-holding capacity, saturated, is 66.8 per cent of the air-dry weight and 56.9 per cent of the volume.

It is regretted that the physical properties of the soils cannot be given in terms of the wilting coefficient. The reason is that it was impossible to make wheat or corn produce sufficient root systems in either the raw humus or the mineral soil. On the decomposed humus (soil [1] above) a single direct determination gave a wilting coefficient of 13 per cent. Calculations from the moisture-holding capacity at saturation, which are probably unreliable for these soils, gave, on the basis of volume, wilting coefficients of 21 per cent for the decomposed humus, 15 per cent for the raw humus. and 12 per cent for the mineral soil.

The acidity of each of these soils was tested by the method which COVILLE gives (**2**, pp. 26–28), and by the TRUOG method (**7**).

The decomposed humus was found to be neutral; the raw humus showed an acidity of 0.002 normal, and the mineral soil an acidity of 0.00017 normal by COVILLE's method. Yet by the TRUOG method the raw humus was strongly acid, and the mineral soil of medium acidity. Tests at the end of the growing season showed only a small diminution in acidity.

The measurements showed that the growth of both fir and spruce was most rapid on the mild humus, effectually disposing of the theory that acidity is required by fir, or favors the fir against the spruce. In fact, the difference in rate between the neutral and acid cultures was greater in fir than in spruce, indicating that spruce withstands acidity better than fir. Growth of both fir and spruce on the mineral soil was slightly more rapid than on the raw humus, except that toward the end of the season some of the spruces on the raw humus began a second growth period which enabled them to pass those on the mineral soil. White pine also did better on the mild humus than on the mineral soil; on the raw humus there were not enough trees of this species for definite conclusions.

The duration of the period of growth in length for the different species is interesting. Fir began elongating on June 1, and stopped on July 10, 40 days later; spruce and pine began on June 5, and did not stop until August 20, a period of 76 days, or nearly twice as long as that of fir. Some of the spruce on the raw humus showed a second growth period lasting until August 30; and yet fir, with its shorter growing period, is a faster growing tree than spruce.

An examination of the root systems of the different species on the different soils, made at the end of October, revealed some suggestive conditions. The roots of all 3 species in the mineral soil showed by far the poorest development. Yet the growth curves for the mineral soil show it to have been a little better than the raw humus. It may be that the nutrients contained by the raw humus are considerably less than in the mineral soil. The poor root development on the mineral soil is perhaps attributable to poor aeration. Since this was not a heavy soil, we have here another indication of the need for an ample oxygen supply on the part of the roots of these 3 conifers (1).

The roots of all species were thicker and thriftier looking on the raw humus than on the mild humus, although fir and white pine were a little more branched on the mild humus. Most striking of all, the roots of all 3 species on the raw humus were still capable of absorption, even at the end of October. This was shown by the presence of a considerable number of the little translucent growing tips which are found during the height of the growing season. On the mild humus growing tips capable of absorption were almost lacking except where the root came in contact with the wood of the flat. In the raw humus the root tips which had ceased to function became brown, while many of those on the mild humus became covered with a white fungus. A black fungus, common in the raw humus of the forest, was found attacking the roots on the mineral soil more than those on the raw humus, indicating that its presence may be due to low vigor on the part of the roots rather than to abundance of spores. The rootlets in the raw humus exhibited a propensity for searching out twigs and cones and growing through them.

Raw humus appears to have an effect on damping off fungus, quite the reverse of what might be expected. In an experiment to determine the effect of drying out, such as the raw humus is subjected to under natural conditions in the open, upon the germination and establishment of *Pinus resinosa*, it was found that on raw humus kept artificially moist there was no damping off, while on the raw humus which received no water except from rain the loss from damping off was 44.4 per cent of the seedlings germinating. That damping off should be so much worse on a dry than on a moist soil is contrary to all previous experience. The explanation is probably to be found in the great abundance of fungus spores in raw humus as compared with ordinary nursery soils, and in the much greater vigor and power of resistance on the part of the seedlings in the moist humus. It is also possible that the constant moisture held enough of the soil acid in solution to prevent germination of the damping off fungus spores, for it is known that treatment of nursery soils with acids before seeding, followed by ample watering during germination, diminishes the losses from damping off.

Experiments were also tried on the effect of these 3 soils on the growth of clover, wheat, and corn. Clover, as might be expected from its sensitiveness to acid, grew very poorly on the raw humus and mineral soil, but throve on the mild humus. In fact, it eventually died back and disappeared on the two former, lasting longer on the mineral soil than on the raw humus. Kubanka wheat did well on the mild humus, except for the shading, while on the raw humus and mineral soil it grew poorly. The dry weights per plant for Kubanka wheat sown June 24 and cropped September 15 were 0.53 gm. for the mild humus as against 0.08 gm. on the raw humus, and only 0.03 gm. on the mineral soil. Corn (Golden Bantam) did so well on the mild humus that it had to be removed to prevent interference with the other experiments, while on the raw humus it produced only 0.09 gm. dry weight per plant, and on the mineral soil 0.13 gm. after growing for more than 3 months. The corn, it will be noticed, did better on the mineral soil than on the raw humus, indicating that this plant is affected more by acidity than by poor aeration. On the other hand, wheat grew better on the raw humus than on the mineral soil; on the former it frequently died down but came up again, while on the latter it showed less power of recovery. This would indicate that wheat is less sensitive to acid than to poor aeration.

Field observations on the root systems of spruce, fir, and white pine showed that detailed studies of roots would probably yield interesting results. Spruce roots form a dense mat in the raw humus or "duff," a mat so dense that hardly a square centimeter under a spruce stand escapes. These rootlets keep growing toward the surface as the humus deepens, those in the lower layers dying back. Hence spruce is in a position to get the first water that reaches the forest floor. The quantity absorbed by these roots must be enormous, and cannot fail to be an important factor in reproduction. Fir roots are characteristically much less branched than those of spruce, and seem to go more into the mineral soil, though they also feed largely in the "duff." This greater penetration may possibly explain in part the ability of fir to grow on drier sites than spruce. White pine absorbs from both the raw humus and the mineral soil. The roots of all 3 species are often

affected by a fungus which produces black threads of mycelium on the root tips. These threads prevent absorption and kill the portion of the root attacked. Yet seedlings appear thrifty even when a large proportion of their roots are affected in this way. Perhaps, since the fungus attacks only the smaller rootlets, the plant is able to develop new rootlets about as fast as the affected ones die off.

A factor of more importance than hitherto recognized is dryness due to the interception of precipitation by the crowns of spruce. The lack of vegetation under a forest of spruce has generally been attributed to lack of light. While light plays an important part, there are probably many cases where lack of moisture rather than lack of light is the determining factor. A rather striking illustration may be cited. Under the crown of a spruce growing in the open was found a patch of forest floor similar in every respect to the forest floor found under dense stands of spruce. Herbaceous vegetation and tree reproduction stopped abruptly at the edge of this spot, yet the crown of this tree was high enough to allow the ground under it to receive ample light. The only vegetation under the crown was a few grasses and asters, light demanding but comparatively drought resistant plants. The bareness of this piece of forest floor was due to lack of moisture, not to lack of light. This was confirmed by moisture tests, which showed that the soil beyond the crown, soil which had been giving up moisture to a thick herbaceous cover all summer and should consequently be drier than a spot which had given up nothing to vegetation and was not subject to high evaporation, possessed 59 per cent of moisture on the basis of air-dry weight as against 20.5 per cent under the crown of the spruce. On the basis of volume, which gives a better conception of the moisture relations in these light soils, the soil in the open contained 19 per cent of moisture as compared with 5.7 per cent under the crown. In another case in a spruce forest the moisture under a small opening in the canopy was 20.9 per cent by volume, as compared with 7.3 per cent under a spruce crown. In both of these cases the soil under the crown was powder-dry to the touch, while that beyond the crowns felt moist. It is evident, therefore, that under the crowns of spruce the soil is

often so dry that neither reproduction nor herbaceous vegetation can become established, no matter how much light it receives.

Counts of the reproduction of spruce, fir, white pine, and cedar, correlated with age, showed that spruce, fir, and white pine become established only at intervals of several years, while cedar comes in every year. The cause of the failure of spruce and fir to become established every year is apparently not related directly to climatic factors, because the season of 1916 was unusually moist and favorable, yet practically no seedlings of these 2 species could be found. Probably the reason for this periodicity in spruce and fir reproduction is to be sought largely in the seed supply. White pine reproduced abundantly in 1916, so that climate can be eliminated as a factor; but since it is equally impossible to eliminate the matter of seed production, the periodicity of white pine reproduction may be due to both the season and the seed supply.

In fir there are indications of a periodicity of reproduction which is of considerably more importance than that due to the seed supply. Under many spruce stands which have reached about middle age, the fir reproduction is nearly all composed of large seedlings approximately 1–3 ft. in height; young seedlings are scarce. In these cases it appears that the fir came in profusely under a set of environmental conditions different from the present ones. Just what these conditions were it is impossible to say without further study. One of them may have been stronger light than at present. Indications of this were found in the fact that some of these cases of fir reproduction occur in stands which were formerly more open than they now are; also, small fir reproduction is abundant in young stands with a full but not very heavy canopy. That light is a factor would be in accordance with Zon's conclusion (8). Another factor may be decreasing moisture, due to the interception of precipitation by the crowns of the spruce trees, and to a fuller use of the humus water by the increasing mat of spruce roots. Whatever the factors are, it seems evident that fir reproduces within a more or less sharply marked range of environmental conditions, and that these conditions are largely controlled by the forest itself.

Each species reproduces only within a certain range of factors. This range is probably a specific characteristic of each tree, possibly of each plant, and appears to be different even for trees growing together in the same association.[2] Determination of this range for even a few of our more important trees would be a valuable contribution.

NEW YORK CITY

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[2] SHREVE (**6**) found that in open vegetation in Arizona the species growing in the same association are subject to different environments.

POLLEN TUBE AND SPERMATOGENESIS IN IRIS

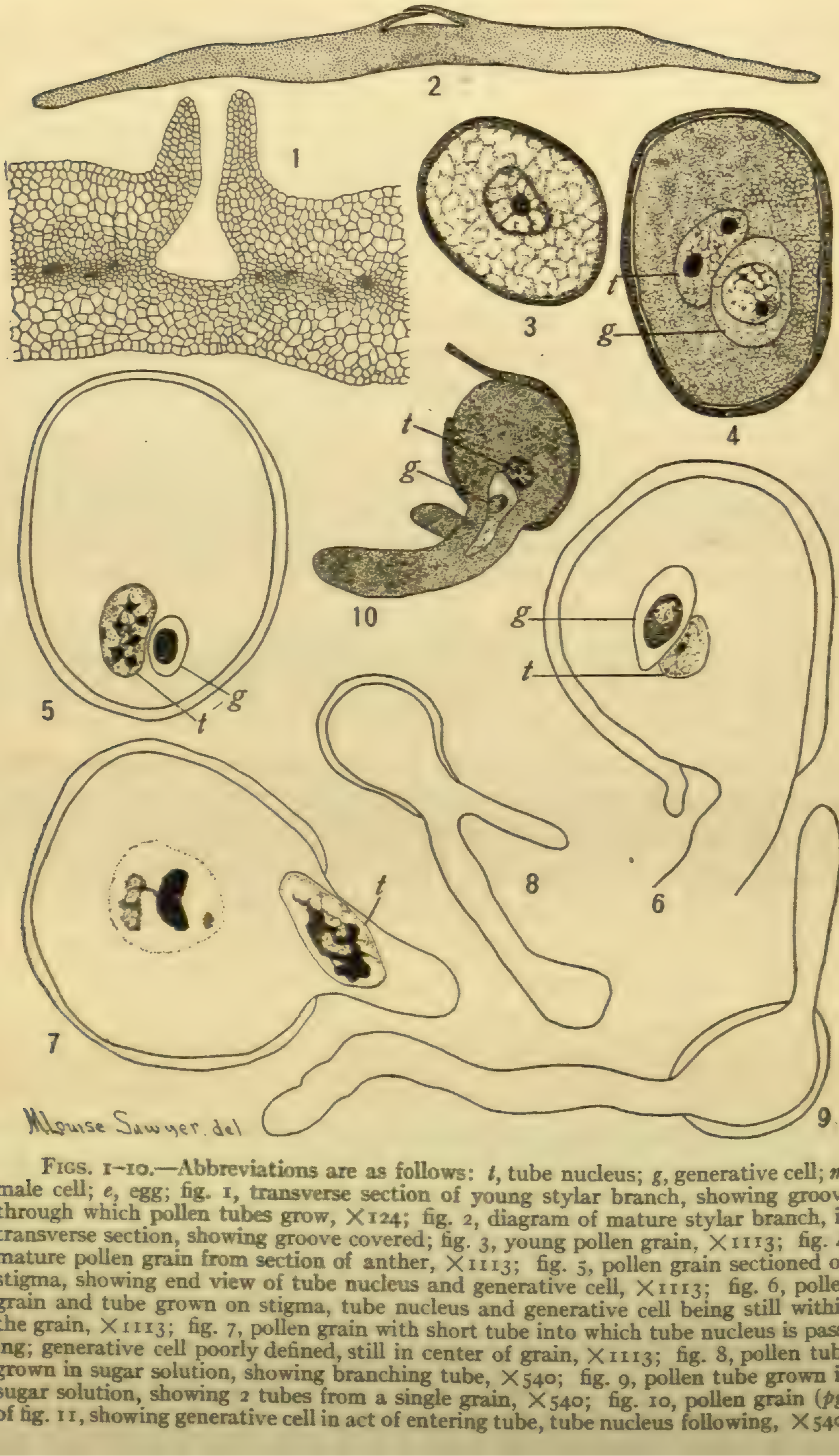
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 235

M. Louise Sawyer

(WITH EIGHTEEN FIGURES)

This study of spermatogenesis had its origin in an attempt to find a satisfactory method of securing prepared as well as living material for demonstrating pollen tubes to a class in embryology. The fact that it was found possible to dissect out the pollen tubes of *Iris versicolor*, so that tubes of various lengths, developed on the stigma and style, became available for study, made it seem advisable to undertake an investigation of the pollen tube of this species. Tubes were also secured in longitudinal sections of style and stigma, and by sowing pollen grains on culture media. Tubes were grown in sugar solutions, the 15–30 per cent proving more satisfactory than weaker solutions. A culture medium was made by adding 30 per cent sugar solution to the sap which oozes from freshly cut stalks, and abundantly from the clasping bases of the leaves. The superiority of the latter over the pure sugar solution lies in the fact that as the tubes grow longer they are less likely, in the cell sap sugar solution, to become distorted. Its disadvantage consists in the difficulty of freeing the tubes from the gelatinous medium.

Flemming's stronger solution proved the most satisfactory killing fluid, and iron-hematoxylin has been the favorite stain. The successful dissection of the tubes is related to the structure of the style. That organ arises from the ovary as a single structure, and at the height of about 1 cm. divides into 3 branches. Cross-sections of a stylar branch (fig. 1) reveal the fact that each branch is traversed by a longitudinal groove. When the flower is mature, the stylar groove is covered by two overlapping outgrowths, arising from the margin of the groove and so forming an inclosed canal, diagrammatically shown in fig. 2. Near the distal end the groove broadens out and terminates in the stigma, which appears as a shelflike projection from the under side of the stylar branch, which



FIGS. 1–10.—Abbreviations are as follows: *t*, tube nucleus; *g*, generative cell; *m*, male cell; *e*, egg; fig. 1, transverse section of young stylar branch, showing groove through which pollen tubes grow, ×124; fig. 2, diagram of mature stylar branch, in transverse section, showing groove covered; fig. 3, young pollen grain, ×1113; fig. 4, mature pollen grain from section of anther, ×1113; fig. 5, pollen grain sectioned on stigma, showing end view of tube nucleus and generative cell, ×1113; fig. 6, pollen grain and tube grown on stigma, tube nucleus and generative cell being still within the grain, ×1113; fig. 7, pollen grain with short tube into which tube nucleus is passing; generative cell poorly defined, still in center of grain, ×1113; fig. 8, pollen tube grown in sugar solution, showing branching tube, ×540; fig. 9, pollen tube grown in sugar solution, showing 2 tubes from a single grain, ×540; fig. 10, pollen grain (*pg*) of fig. 11, showing generative cell in act of entering tube, tube nucleus following, ×540.

is continued beyond the stigma. By removing the covers of the groove the canal containing the tubes lies exposed, and they can be removed with needles.

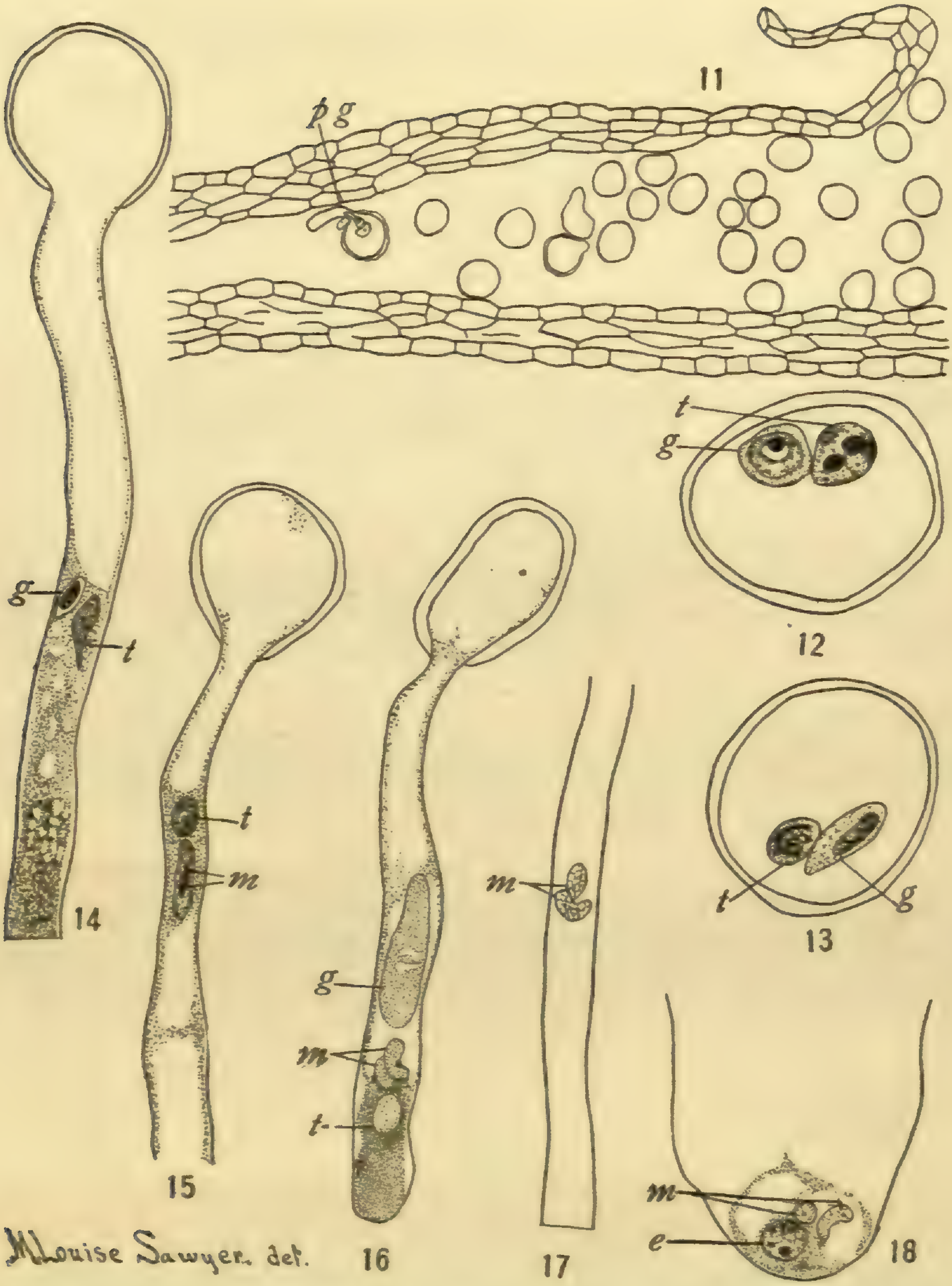
Tubes grown in hanging drops of culture media show a rather striking tendency to grow from the margins of the drop in groups, the tubes being in close contact with each other. This fact is suggestive when associated with the fact that from the stigma the pollen tubes converge in two lines and traverse the stylar branch at the margins of the groove, where the space is most restricted (fig. 2). It has usually been assumed that the pollen tube is guided in its direction of growth by chemotaxis. These observations suggest that in *Iris* contact stimulus may be an effective guide. Further investigation of this point is purposed.

The structure of the newly formed pollen grain (fig. 3) was studied in sections of the anther. The division of the microspore nucleus was not observed, but it occurs in the anther, as would be expected, and the generative cell is organized before dehiscence (fig. 4). The generative cell is slender, elongated, and somewhat pointed when seen from the side (figs. 6, 13), and is frequently overlaid by the tube nucleus (figs. 4, 5). In this condition the pollen is shed. Hand pollination was successfully performed. Usually cross-pollination was effected, but it was demonstrated that pollen would produce abundant tubes on the stigma of the stylar branch under which it was located. Observation on the rate of growth of pollen during 7 hours after pollination was made, and their lengths measured with an ocular micrometer. Table I indicates results.

TABLE I

Time after pollination	Length of tubes
1 hour	0.1–0.6 mm.
3 hours	2–2.5
5 hours	4.5–5
7 hours	8–9.5

The acceleration in the rate of growth, as indicated by these data, is interesting. In 9–10 hours tubes were observed at the base of the stylar branch. After 20 hours tubes were discovered



Louise Sawyer, del.

FIGS. 11–18.—Abbreviations are as follows: *pg*, pollen grain; *t*, tube nucleus; *g*, generative cell; *m*, male cell; *e*, egg; fig. 11, section of stigma with pollen grains, some of which are growing tubes, ×140; figs. 12 and 13, pollen grains in anther, showing appearance of tube nucleus and generative cell from different views, × 1113; fig. 14, pollen tube with tube nucleus in act of passing generative cell, ×540; fig. 15, pollen tube with generative cell containing 2 male nuclei preceding tube nucleus, ×540; fig. 16, pollen tube with tube nucleus and 2 male nuclei near tip, expanded cytoplasm of generative cell above showing cavities from which male nuclei escaped, ×540; fig. 17, portion of a long pollen tube, showing 2 male nuclei free in tube, ×540; fig. 18, end of embryo sac, with egg and 2 male nuclei, ×540.

within the ovary. The pollen tubes occasionally branch. This was observed both in tubes grown on the stigmas and in those grown on nutrient solutions (fig. 8). In the cell sap sugar solution some grains produced 2 tubes (fig. 9), indicating 2 germination spots.

Longitudinal sections of hand pollinated stigmas (fig. 11) show pollen grains (fig. 5) which have essentially the characteristics of the grains in the dehiscing anthers, and among them grains which are producing pollen tubes. A tube (fig. 10) caught just as the tube nucleus and the generative cell were passing the tube distinctly shows the latter preceding, contrary to the order that is usually reported. In other cases the tube nucleus led the way from the grain into the pollen tube (fig. 7). The number of cases thus far observed at just this stage is not sufficiently large to warrant a statement as to which of these conditions is prevalent in *Iris versicolor*. Apparently it is usual for the tube nucleus to soon gain the leading position. One instance (fig. 14) of the tube nucleus in the act of passing the generative cell was observed. The peculiar elongated and pointed anterior end of the tube nucleus is very interesting and suggests a self-motile body.

The generative cell certainly usually passes into the tube before its nucleus divides to form the male nuclei, but occasional grains suggest the possibility that it sometimes divides in the grain. The division of the generative cell has not been observed, but in tubes dissected from the stigma, and in those grown in the culture media, the generative cell has frequently been seen apparently containing 2 nuclei (fig. 15*m*). The contents, which microchemical tests show contain much starch, stain so heavily that it is difficult to differentiate the nuclei satisfactorily. The material seems to indicate a somewhat wide range in the position of the generative cell in the tube at the time division of its nucleus occurs.

A tube (fig. 16) but a fraction of a millimeter in length appeared to contain the tube nucleus, behind it the generative cell cytoplasm, and between them, free in the tube, the 2 male nuclei. In a group of dissected tubes which were about 14 mm. long, a tube contained free male nuclei (fig. 17) about halfway between the grain and the end of the pollen tube. At 79 hours after pollination such male nuclei were seen in the embryo sac (fig. 18). It is noticeable that

in all of these cases no cytoplasm could be detected in association with the male nuclei, and also that in all views of these male nuclei one of them appears larger than the other, the larger one slightly vermiform. It remains to determine whether this apparent difference is real or whether in each case one of the nuclei is seen from the end. In the embryo sac section it seems probable that the smaller appearing one is the one likely to fertilize the egg.

Summary

1. The style of *Iris versicolor* is traversed by a longitudinal groove through which the pollen tube grows.

2. It is possible to remove pollen tubes from style and stigma and to grow pollen tubes in nutrient solutions.

3. Measurements indicate that there is an accelerated rate of growth of pollen tubes.

4. Pollen tubes may branch or a grain may produce two tubes.

5. The generative cell is an elongated, somewhat pointed cell, and may precede the tube nucleus from the tube.

6. Production of the male nuclei usually occurs after the generative cell has entered the tube.

7. The male nuclei may leave the generative cytoplasm, and were seen free in the tube.

8. The male nuclei were observed in the embryo sac 79 hours after pollination.

The writer is indebted to Professor H. D. DENSMORE of Beloit College for suggestions which led to the undertaking of this investigation. Acknowledgments are also due Professor JOHN M. COULTER and Dr. CHARLES J. CHAMBERLAIN for helpful criticism during the progress of this work.

BELOIT COLLEGE
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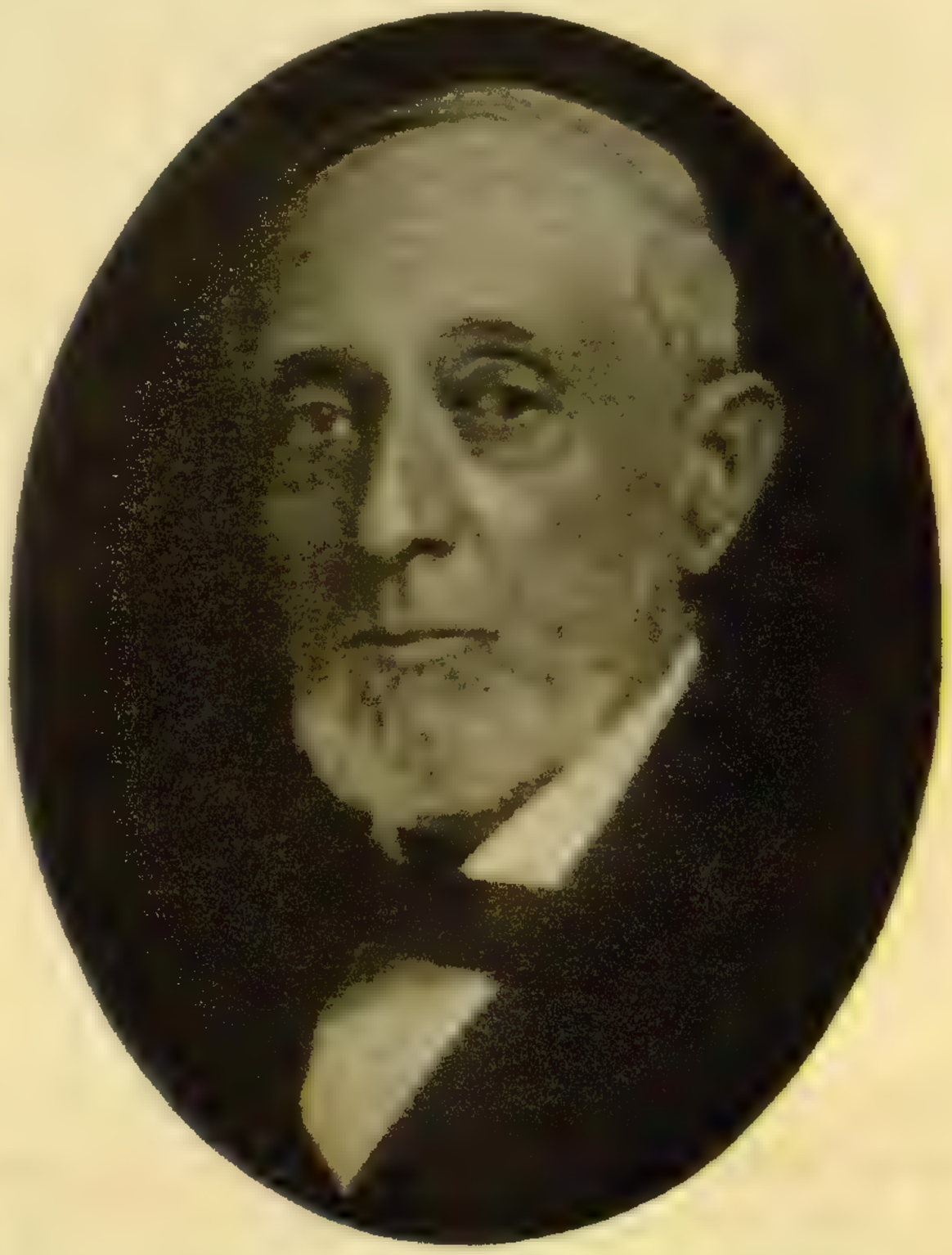
BRIEFER ARTICLES

ELLSWORTH JEROME HILL

(WITH PORTRAIT)

E. J. HILL was a well known figure to the Chicago group of botanists. For over 40 years he studied the plants of the Chicago region. No one was more familiar with them, or had brought so many of them to general notice. He was much more than a collector and taxonomist; in addition, he was an ecologist before ecology was recognized as a subject.



He was born at LeRoy, New York, December 1, 1833, and died in Chicago, January 22, 1917. His early life was spent on a farm, in which environment he began to develop his love of natural history. At the age of 19 he was taken suddenly lame by an affection of the knee, and during the rest of his long life, with intervals of relief, this trouble accompanied him. After his first trouble, to get away from the northern winter, he went to Mississippi and taught for three years in a woman's college at Grenada, afterward returning to New York. In 1860 he began a theological course in Union Theological Seminary, graduated in 1863, and engaged in pastoral work until 1869, when another attack of lameness incapacitated him for two years. He then became a teacher again, first in the high school of Kankakee, Illinois, for four years, and then for fourteen years in the high school of Englewood, now a part of Chicago. In 1888 he gave up teaching and devoted himself almost entirely to botany.

Hill's experience as a persistent field student is a lesson in patience and courage. His numerous field trips on crutches and afterward with canes; his devices to overcome the handicap of lameness while collecting; his persistence in making these trips even when he paid a severe penalty for exposure or over-exertion—all testify to the spirit of the man. During his later years he was a constant and welcome visitor at the weekly meetings of the Botanical Club of the University of Chicago, and was always intensely interested in the various phases of modern botany. His mind was open and progressive, turned toward the future of his subject rather than toward the past.

His bibliography as published includes 162 titles, ranging in time from 1870 to 1916, and covering all the phases of botany that would attract the attention of an active field man with broad interests. This journal published 34 of his titles, the majority of them during the decade 1880–1890, and the last one in 1910. Certain genera received his critical attention, among them being *Potamogeton*, *Carex*, *Quercus*, *Prunus*, *Salix*, and *Crataegus*. Taxonomists will recognize the fact that these are difficult genera, but it was their difficulty that attracted.

The Hill Herbarium, which is said to include 16,000 sheets, the accumulation of years of critical work, has been secured by the University of Illinois. It represents probably the most valuable single collection of Illinois plants, especially of the Chicago region, and it is fortunate that it has been made available in a public institution.—J. M. C.

RESISTANCE OF SEED COATS OF ABUTILON THEOPHRASTI TO INTAKE OF WATER

In the fall of 1910 I gathered seeds of *Abutilon Theophrasti* (velvet leaf) near Manhattan, Kansas, placed them in vials of 100 seeds each, covered them with water, and stoppered the vials. The results in the various vials up to the present time have been very similar.

In one vial 32 seeds had swollen within the first 3 weeks and were removed from the vial. During the past 6 years 22 of the remaining seeds have swollen and were removed, sometimes in a decaying condition, as the vial was seldom examined. In December 1916 a desk in which the vial was stored was removed to a small room and placed near a radiator where the temperature rose much higher than any to which the seeds had previously been subjected. Within a week 22 seeds had swollen. These were removed and placed under germinating conditions

and germinated as quickly and apparently with as much energy as fresh seeds. Of the original 100 seeds 24 still remain intact.

In order to ascertain the resisting power of the seed coats of velvet leaf to water at various temperatures, in December 1916 I collected seeds from plants still standing in the field. Most of the seeds at that time had dropped from the pods, and those I found were mostly hard-coated. In one case only 3 seeds in 100 had swollen after soaking 48 hours at room temperature. Two lots of seeds of 100 each were selected and each lot was placed in a small vial. The vials were then filled with water at a given temperature and suspended in Dewar flasks filled with water at the same temperature. At the end of 6 hours the vials were removed, the seeds that had swollen were counted, removed, and the remaining seeds were returned for a similar period at a temperature 5° higher, and so on until all the seeds had swollen. The temperature of the flask for each period was kept practically constant. The seeds in flask no. 1 were started at 30° C., and in no. 2 at 35° C. The results are indicated in table I.

TABLE I

Flask no. 1			Flask no. 2*		
Temperature	Time in hours	Number swollen	Temperature	Time in hours	Number swollen
30° C.	6	8	35° C.	6	15
35	6	9	40	6	13
40	6	19	45	6	12
45	6	17	50	6	13
50	6	8	55	6	13
55	6	5	60	6	9
60	6	12	65	6	10
65	6	7	70	6	5
70	6	10	75	6	4
75	6	5			
Total		100	Total		94

*6 seeds were lost.

These results indicate a wide range in the resisting power of the coats of these seeds to the intake of water, and no doubt many of the more resistant may lie in the soil many years before germination can take place.—Wilmer E. Davis, *Kansas State Agricultural College.*

CURRENT LITERATURE

BOOK REVIEWS

Contributions to plant physiology

In a little booklet[1] of 95 pages is given the work of the department of plant physiology at Johns Hopkins University. LIVINGSTON gives a description of the department, discussing the aims and the work in progress or so far accomplished, to which is appended a list of the publications from the laboratory arranged by years. The rest of the book is devoted to abstracts of work in progress or recently completed. A list of the authors and titles of these articles will give an idea of the number of investigators in the department, along with the nature and scope of the problems being covered: B. E. LIVINGSTON, Atmometric units; The vapor tension deficit as an index of the moisture condition of the air; Incipient drying and temporary and permanent wilting of plants, as related to external and internal conditions; B. E. LIVINGSTON and E. E. FREE, The effects of deficient soil oxygen on the roots of higher plants; E. E. FREE, The effect of aeration on the growth of buckwheat in water cultures; Symptoms of poisoning by certain elements in *Pelargonium* and other plants; E. E. FREE and S. F. TRELEASE, The effects of certain mineral poisons on young wheat plants in three-salt nutrient solutions; The effect of renewal of culture solutions on the growth of young wheat plants in water cultures; S. F. TRELEASE, The relation of the concentration of the nutrient solution to the growth of young wheat plants in water cultures; H. S. FAWCETT, Preliminary note on the relation of temperature to the growth of certain parasitic fungi in cultures; The geographical distribution of the citrus diseases melanose and stem-end rot; HOWARD PULLING, Some unusual features of a sub-arctic soil; The experimental determination of a dynamic soil-moisture medium; F. M. HILDEBRANDT, Leaf product as an index of growth in soy bean; A method for approximating sunshine intensity from ocular observations of cloudiness; F. S. HOLMES, Moisture equilibrium in pots of soil equipped with auto-irrigators; E. S. JOHNSTON, Seasonal variations in the growth rates of buckwheat plants under greenhouse conditions; W. E. TOTTINGHAM, On the relation of chlorine to plant growth.

Aside from many individual contributions, the work of the laboratory groups itself largely about three large topics: water relations of plants, inor-

[1] Contributions to Plant Physiology, the Department of Plant Physiology, Johns Hopkins University, Reprint from the Johns Hopkins University Circular, March 1917.

ganic salt relations of plants, and relation of plants to climatic conditions. A quotation from the book expresses the point of view under which the work of the laboratory is being conducted.

To summarize the last few paragraphs, our operations have been and are directed toward a dynamic analysis of plant activity. The point of view here employed may perhaps be envisaged if the reader will regard the living plant in somewhat the same general way as he might any complex machine, such as a gasoline motor, for example. To understand its working, one must understand how and how much various conditions may effect a machine; in short, he must become an engineer with respect to that particular mechanism. Dynamic plant physiology may be said, then, to be engineering science as applied to the living plant. It can progress, then, only through quantitative studies, through the comparison of efficiency graphs and curve-tracings made by recording instruments, through the mathematical interpretation of relations between conditions and process rates, etc., and it is with just this sort of studies that our investigations have to do.

It might be well if scientific departments generally issued such statements of their aims and progress.—Wm. Crocker.

NOTES FOR STUDENTS

Rhizoctonia.—In a paper constituting a continuation of former studies of the genus *Rhizoctonia*, Eriksson[2] adds an account of two further forms, *R. Medicaginis* DC. and *R. Asparagi* Fuckel. The paper deals largely with historical and descriptive matter; the chief interest, however, centers in the questions relating to the taxonomy and morphology of these fungi. In 1851 the Tulasne brothers united *R. crocorum* DC., *R. Medicaginis*, and most of the forms of *Rhizoctonia* occurring on other hosts under one species, which they called *R. violacea* Tul. Eriksson, basing his judgment partly upon the association of *Leptosphaeria circinans* (Fuckel) Sacc. with *R. Medicaginis* reported in the literature and also observed by him, and partly on the resemblance of the hyphae of the germinating spores of *Leptosphaeria* to the mycelium of *Rhizoctonia*, concludes that *Rhizoctonia Medicaginis* has an ascogenous fruiting stage and therefore is distinct from *R. violacea*, which he had doubtfully associated with *Hypochnus violaceus* (Tul.) Erikss. Regarding the specificity of *R. Asparagi*, Eriksson concludes, as a result of cross-infection experiments conducted by means of infected soil in deep concrete frames, that this fungus is probably a distinct form whose position cannot be determined until something is known of the perfect stage.

Duggar,[3] in a paper published almost simultaneously with that of Eriksson, confirms the view of the brothers Tulasne that all the forms of the violet

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[2] Eriksson, J., Fortgesetzte Studien über *Rhizoctonia violacea* DC. Arkiv. Bot. 12:1–31. 1915.

[3] Duggar, B. M., *Rhizoctonia crocorum* (Pers.) DC. and *R. Solani* Kühn (*Corticium vagum* B. and C.), with notes on other species. Ann. Mo. Bot. Gard. 1:403–458. 1915.

root-felt fungus found on crocus, alfalfa, and many other hosts (of which 54 are listed by him) belong to a single species, to which the name *Rhizoctonia crocorum* (Pers.) DC. must be applied as long as the fruiting stage remains unknown. This view is based upon a critical examination of the data in the literature and an extensive study of living material and herbarium specimens. He regards the evidence thus far presented as insufficient for the identification of the perfect stage of the fungus. Unlike ERIKSSON, he finds no resemblance between the mycelium produced by spores of *Leptosphaeria circinans* which he germinated and the hyphae of *R. crocorum*. DUGGAR further gives an account of *Rhizoctonia Solani* Kühn, which is the more common of the two species in America where it is the widespread cause of "damping off" of seedlings and cuttings and root-rot of various crops. This species is clearly differentiated from the violet *Rhizoctonia* by characteristics of the mycelium and the sclerotia, as well as by the effects produced on the host plants. Furthermore, evidence seems to be sufficient that the perfect stage of this organism is *Corticium vagum* B. and C. In a later paper,[4] as a result of a study of the data in the literature, this fungus is identified with the "Vermehrungspilz" common in the seed beds and cutting beds of Germany and France, and also with the "Mopopilz," causing considerable damage to the seed beds of cinchona in Java. The failure to recognize *Rhizoctonia Solani* as the general cause of the "damping off" of seedlings in Germany and France, as well as in Java, is attributable to wrong determinations of the European seed bed fungus and the cinchona fungus of Java.

Among other differences mentioned by DUGGAR between *Rhizoctonia Solani* and *R. crocorum* is the difference in their capacity for growing on artificial media. *Rhizoctonia Solani* grows readily on all the common culture media, while *R. crocorum* had not, up to that time, been successfully grown. Recently, however, DIEHL[5] reports successful cultures of the fungus from detached masses of mycelium. The fungus grew with extreme slowness, and only in one instance was a pure culture obtained.

A thorough and comprehensive study of the parasitic Rhizoctonias of the United States has been reported by PELTIER.[6] The chief features of the report are (1) a general historical account, (2) a discussion of the morphology of the fungi, (3) a complete tabulation of the data relating to the hosts, occurrence, and distribution of *R. Solani* and *R. crocorum* in the United States, with notes on the distribution of these organisms in other countries, (4) a description of the disease induced by these fungi in different plants, (5) the results of

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[4] DUGGAR, B. M., *Rhizoctonia Solani* in relation to the "Mopopilz" and the "Vermehrungspilz." Ann. Mo. Bot. Gard. **3**:1–10. 1916.

[5] DIEHL, W. W., Notes on an artificial culture of *Rhizoctonia crocorum*. Phytopathology **6**:336–340. 1916.

[6] PELTIER, G. L., Parasitic Rhizoctonias in America. Univ. Ill. Agric. Exp. Sta. Bull. **189**:279–390. *figs.* 23. 1916.

cross-infection experiments with *R. Solani*, and (6) a description of the growth of this fungus in various media.

The numerous cross-infection experiments carried out with *Rhizoctonia Solani* are of special interest. Strains of the fungus from some 30 species of plants were used to infect carnations in several stages of growth, from the cutting to the mature plant, both under glass and in the field. A number of other plants also were infected with various strains of *Rhizoctonia*. The results of all these cross-infection experiments can best be stated in the author's own words: "From these inoculation experiments with a large number of different types of plants, we must conclude that all the strains studied, which were obtained from a wide range of hosts of diverse geographical origin, can attack the same species of plant and produce the same characteristic symptoms. No marked specialization was noted in any of the strains. Thus, all the strains studied can be included under one form, *Rhizoctonia Solani* Kühn. The inoculation experiments show further that the virulence of *R. Solani* is very variable, as is also the degree of resistance of the various host plants, both depending upon a number of factors." A study of the growth characteristics confirmed this general conclusion. Strains isolated from the same host species showed differences as great as those between strains isolated from different species.

MATZ[7] has described a form of *Rhizoctonia* occurring on the leaves and stems of *Ficus Carica* at Gainesville, Florida. This form is regarded by him as a distinct species, *R. microsclerotia* Matz. Aside from its foliicolous habit, it does not appear to differ essentially from *R. Solani*, which MATZ found was also capable of infecting fig leaves, without producing sclerotia, however. In a single experiment the fig fungus failed to infect seedlings of the cowpea, while *R. Solani* killed 90 per cent of the young plants.—H. HASSELBRING.

The number of chromosomes.—Partial lists of the number of chromosomes reported by various observers for various plants have been published from time to time, but the lists have been incidental and usually no authority has been cited. The most complete of these earlier lists is that of TISCHLER (Progressus Rei Botanicae **5**:164–284. 1915). ISHIKAWA[8] has compiled the most complete list ever published, and in each case has cited the authority. Besides, he has counted the chromosomes in several forms which are here reported for the first time. The theoretical interpretation of chromosomes and their value in phylogenetic studies will be considered later. In sexual forms, the x and $2x$ numbers are cited in separate columns; in asexual forms, the numbers are cited in the x column.

A mere glance at ISHIKAWA's tables reveals some interesting facts. In the Flagellates most of the numbers are preceded by the sign $\pm$, indicating an

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[7] MATZ, J., A *Rhizoctonia* of the fig. Phytopathology **7**:110–117. 1917.

[8] ISHIKAWA, M., A list of the number of chromosomes. Bot. Mag. Tokyo **30**: 404–448. *figs.* 32. 1916.

estimate rather than an exact count. All of the Myxomycetes show 8 as the *x* number; in the diatoms only 3 genera are cited, the *x* numbers being 4, 8, and 64, the latter with 128 as the *2x* number; in the Conjugatae 12 is the prevailing number, and in most cases the *2x* is not cited; in the Chlorophyceae the *x* numbers are various, ranging from 6 to 32, but no *2x* numbers are given; in the Phaeophyceae the *x* numbers are 16, 18, 22, 24, and 32, with the expected *2x* numbers; in Characeae the *x* numbers are 21 and 16, but no *2x* numbers are cited; in Rhodophyceae 8 forms are given, with *x* numbers ranging from 7 to 24 and with the corresponding *2x* numbers. In the fungi the numbers are low and the *2x* numbers are given in comparatively few cases; the minimum *x* number is 2, and it has been noted in 2 species; 4 appears in 24 species; very few have more than 8 as the *x* number; and the maximum number (16) is cited in 6 cases. In the bryophytes 8 is the prevailing *x* number, having been noted in 12 species, while 4 has been counted in 6 species, and 12 in one case and 6 in another. The *2x* numbers have been counted in nearly all cases. In the mosses the *x* number ranges from 6 to 24, with 6 (counted in 6 species) as the prevailing number. In the pteridophytes the numbers are comparatively high, the *x* number ranging from 4 to 120, and 24 of the 35 species cited have 32 or more, while only one (*Salvinia*) shows the minimum number. In the gymnosperms 12 and 24 have appeared so constantly as the *x* and *2x* numbers that any other countings need to be very thoroughly supported; 34 species with 12 as the *x* number are cited, and 3 which are cited as having 8 chromosomes are now known to have 12, but there are still 6 species in which the number 8 has not been disputed. Other numbers are 6, 10, and 16. Of the 44 pages of citation, 28 are devoted to angiosperms. The *x* number ranges from 3 in *Crepis virens* to 45 in *Chrysanthemum arcticum*. The average number is higher in the dicotyledons than in monocotyledons, and the most frequent *x* numbers are 8, 12, and 16.

The list is valuable not only for the systematically arranged citations of chromosome counts, but also because it brings together a considerable portion of the cytological literature in which the chromosome appears either as a principal or as an incidental feature.—CHARLES J. CHAMBERLAIN.

Stomatal regulation.—From rather extensive experimentation upon ivy and laurel (*Prunus Laurocerasus*), DARWIN[9] concludes that transpiration is regulated by size of stomatal aperture, and that "LLOYD's dictum 'their (stomates) regulatory function is almost nil' " must be abandoned. The stomatal aperture was determined by use of his well known potometer, which determines the rate of flow of air through the stomates under a given pressure. The rate of transpiration was determined by weighing or by use of the potometer. Modification of stomatal aperture was induced by normal daily changes or

[9] DARWIN, F., On relation between transpiration and stomatal aperture. Phil. Trans. Roy. Soc. London B **207**:413–437. 1915.

by shorter periods of darkness and light. Humidity of the air was figured to a standard.

Potometer determination of stomatal aperture involves mass movement of air through the stomates under differential pressure, while transpiration involves static diffusion of water vapor through the stomates. To clear up the physics of the problem, DARWIN gives two quotations from Sir J. LARMOR: "The speed of diffusion through a narrow aperture between two open spaces is proportional to its diameter. The speed of a stream of air through such an aperture, between open spaces having different pressures on them, is proportional to its area if the effect of viscosity can be neglected, but proportional to the $\frac{3}{2}$ power of its area if viscosity is preponderant. Which of these conditions prevails, or whether the circumstances are intermediate, in a given case, depends upon the diameter of the aperture." "Diffusion through a long pipe or channel varies as the area, and flow through it depends upon a reduced area owing to the flowing air adhering to the walls of the tube; in fact it varies as the square of the area if viscosity is predominant. Thus if this be the case, provided the channels are of fairly uniform width, transpiration would be proportional to the square root of flow, the same law as that obtained for the case of holes in a thin plate." DARWIN believes the second assumption most nearly represents the situation, for the first applies only to tubes whose lengths are less than one-fifth of their diameter. As might be deduced from either of the physical laws just stated, the author has made one curve by plotting the square root of the rate of potometer flow, and another by plotting the rate of transpiration for various stomatal apertures, and for 18 separate experiments finds general agreement between the curves, although there are many minor discrepancies.

One regrets that the experiments were not carried out in closely controlled temperature and humidity conditions, which might go far to eliminate minor discrepancies. Evaporimeter records and measured light intensities might also aid in explaining these discrepancies. Much has been done since 1900 to put the material and energy exchanges between the leaf and the air upon a sound physical basis, and this is a noteworthy step in that direction. One is impressed by the excellent scientific spirit of the writer, and by the considerate way in which he deals with those who differ from him.—WM. CROCKER.

Sweet potatoes during storage.—HASSELBRING and HAWKINS[10] made a study of the course of the carbohydrate transformations in sweet potatoes (*Ipomoea Batatas*) during storage. The data indicated that a more rapid transformation of starch into sugar took place immediately after the roots were dug than at subsequent periods. This suggested intensive investigation relative to the effect of cessation of leaf activity and the effect of different temperatures on the progress of carbohydrate transformations. The study was

[10] HASSELBRING, H., and HAWKINS, L. A., Carbohydrate transformations in sweet potatoes. Jour. Agric. Research **5**:543–560. 1915.

planned so as to include 3 series of experiments. In the first series samples of freshly dug potatoes were collected and cut lengthwise into two equal parts. One set of the samples was used immediately for the determinations of moisture, sugar, and starch. The corresponding halves were divided into 3 sets and each set stored at a different temperature for 12 days before similar determinations were made. The samples were stored at 30, 15.5, and 5° C. For a check a number of whole potatoes were subjected to the same conditions. The second series was a duplicate of the first, except that the potatoes were dug about 2 weeks later. This series would show any change occurring in the growing potatoes after the first series was harvested. The third series of experiments was modified so as to determine the effect of removal of the vines on the carbohydrate transformations. The roots were not harvested until 10 days after a killing frost.

HASSELBRING and HAWKINS pointed out that to the rate of carbohydrate transformations in stored sweet potatoes the Van't Hoff temperature law was applicable. In general, at 30° C. starch hydrolysis was rapid at first and soon reached an end point. At 15°.5 C. a more normal rate of transformation took place, tending toward a state of completion. The hydrolysis at 5° C. was markedly retarded. In spite of the utilization of reducing sugar in respiration, HASSELBRING and HAWKINS were able to show a marked accumulation at first and very little subsequent accumulation. The concentration of the reducing sugar was found to be comparatively low during the period of storage. There was a lag in accumulation of cane sugar, associated with the increase of reducing sugar. The data suggested that the mode of carbohydrate transformation in stored sweet potatoes was from starch to reducing sugar, which resulted in the formation of cane sugar as the end product. On studying the effect of the vines on transformations, it was found that during their activity the sugar content remained low. As soon as the flow of materials was checked by removal of the vines, the usual transformations as found in storage of sweet potatoes manifested themselves.

HASSELBRING and HAWKINS[11] have pointed out that the internal changes during storage must play an important rôle in susceptibility to decay. Aside from the theoretical significance, it seems that this mode of attack on storage problems of this nature will be of economic value.—FRED W. GEISE.

Taxonomic notes.—BRITTON,[12] in continuation of his studies of West Indian plants, has described new species in *Cleome*, *Chamaecrista* (3), *Leucocroton* (3), *Passiflora* (3), *Rondeletia* (10), *Eriocaulon* (3), *Dupatya*, *Pilea*, *Ichthyomethia*, *Castelaria*, and *Stenostomum* (2).

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[11] HASSELBRING, H., AND HAWKINS, L. A., Physiological changes in sweet potatoes during storage. Jour. Agric. Research **3**:331–342. 1915.

[12] BRITTON, N. L., Studies of West Indian plants. IX. Bull. Torr. Bot. Club **44**:1–37. 1917.

FAWCETT and RENDLE[13] have described new species of *Tephrosia*, *Cassia*, and *Erythroxylum* from Jamaica.

GATES[14] has described a new species of *Oenothera* (*O. novae-scotiae*) from Nova Scotia. It is related to *O. muricata*, but is distinct in leaf, stem, and bud characters, especially as to pigments. The species was studied in connection with the germination of 1000 of its seeds.

GREENMAN,[15] in continuation of his studies of *Senecio*, has presented § AUREI. The section includes 48 species, 5 of which are new, the descriptions being accompanied by a full bibliography and liberal citations of exsiccatae, especially such as occur in American herbaria. The same author[16] has also described a new vinelike *Senecio* (*S. Hollickii*) from Jamaica, collected by BRITTON and HOLLICK in 1908.

Miss HILL[17] has described a new species of *Spirogyra* collected in the basin of an old fountain in Seattle, Wash. It is named *S. gigantica* on account of its size, the filaments being 173–188 μ in diameter, the cells being 1–2 diameters long, and with 4–6 chloroplasts. It most nearly resembles *S. crassa*.

HUBBARD[18] has described a new species of *Agropyron* (*A. acadiense*) from Cape Breton, Nova Scotia, related to *A. Smithii* Rydb.

NAKAI,[19] in continuation of his studies of the plants of Japan and Corea, has described 15 new species in several genera, and proposes the following new genera: *Pentactina* (Spiraeaceae) and *Polakiastrum* (Scrophulariaceae).

OLIVE and WHETZEL,[20] in connection with a study of the parasitic fungi of Porto Rico, describe *Botryorhiza* and *Endophylloides* as new genera, and also 4 species of *Endophyllum* as new combinations, formerly referred to *Aecidium*.

PRAEGER,[21] in the course of a revision of *Sedum* as found in cultivation, has described 8 new species.—J. M. C.

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[13] FAWCETT, W., and RENDLE, A. B., Notes on Jamaica plants. Jour. Botany **55**:35–38. 1917.

[14] GATES, R. R., A new evening primrose. Trans. Nova Scotia Inst. Sci. **14**:141–145. *figs. 2*. 1916.

[15] GREENMAN, J. M., Monograph of the North and Central American species of the genus *Senecio*. Part II. Ann. Mo. Bot. Gard. **3**:85–194. *pls. 3–5*. 1916.

[16] ———, A new *Senecio* from Jamaica. Ann. Mo. Bot. Gard. **3**:201, 202. 1916.

[17] HILL, GRACE A., *Spirogyra gigantica*, n.sp. Puget Sound Marine Sta. Publ. **1**:198. *figs. 2*. 1916.

[18] HUBBARD, F. TRACY, A new *Agropyron* from Cape Breton. Rhodora **19**:15–17. 1917.

[19] NAKAI, TAKENOSHIN, Notulae ad plantas Japaniae et Coreae. XIII. Bot. Mag. Tokyo **31**:3–30. 1917.

[20] OLIVE, E. W., and WHETZEL, H. H., *Endophyllum*-like rusts of Porto Rico. Amer. Jour. Bot. **1**:44–52. *pls. 1–3*. 1917.

[21] PRAEGER, R. LLOYD, Some new species of *Sedum*. Jour. Botany **55**:38–44. 1917.

Enzyme activity of fungi.—With a view of ascertaining the manner of destruction of wood by *Lenzites saepiaria*, ZELLER[22] has made a general study of the enzymes in the mycelium and sporophores of that fungus. Enzyme preparations of the mycelium were made by extraction of dried and ground cultures of the fungus grown on sawdust. The enzyme mixture precipitated from the extract by means of alcohol was collected on filter paper and preserved dry. Preparations from the fruit bodies were made in a similar manner. From the activities exhibited by the powder thus obtained, the author concludes that the following groups of enzymes are present in the mycelium and sporophores of *Lenzites saepiaria:* (1) of the esterases chiefly those affecting the hydrolysis of the esters of the lower fatty acids; (2) of the carbohydrases, maltase, invertase, raffinase, diastase, innulase, ligninase (by which the author designates CZAPEK'S "hadromase"), cellulase, hemicellulase, and pectinase; (3) of other enzymes, emulsin, tannase, urease, hippuricase, nuclease. proteinases, rennetase, oxidase, and catalase.

It is of interest to note that in cultures of the fungus on resin agar emulsions containing a gradually increasing percentage of resin, growth was only slightly depressed in emulsions containing up to 50 per cent of resin. In emulsions containing over 50 per cent of resin growth is sharply depressed, while in those containing over 85 per cent growth is practically inhibited.—H. HASSELBRING.

Texas root rot.—DUGGAR[23] reports the finding of a conidial stage of the Texas root rot fungus, *Ozonium omnivorum* Shear, one of the most destructive fungous diseases of the cotton crop. The conidia-bearing hyphae usually occur in patches on the bare ground between the rows of plants and only rarely in connection with the roots themselves. They are borne on swollen or club-shaped branches recalling the conidiophores of some species of *Botrytis*. The spore powder which covers the ground of the fertile patches is pinkish buff. The fungus is tentatively placed in the hyphomycete genus *Phymatotrichum* as *P. omnivorum* (Shear) Duggar.—H. HASSELBRING.

Vegetation of Long Island.—HARPER[24] has published a list of the plants found growing on a part of Long Island which is really within the limits of New York City. It will serve for comparison with adjacent areas and as a record of the natural vegetation of an area which may soon become in reality a part of a densely populated city.—GEO. D. FULLER.

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[22] ZELLER, S. M., Studies in the physiology of the fungi. II. *Lenzites saepiari* Fries, with special reference to enzyme activity. Ann. Mo. Bot. Gard. **3**:439–512. *pls. 2*. 1916.

[23] DUGGAR, B. M., The Texas root rot fungus and its conidial stage. Ann. Mo. Bot. Gard. **3**:11–23. 1916.

[24] HARPER, R. M., The natural vegetation of western Long Island south of the terminal moraine. Torreya **17**:1–13. 1917.

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THE

BOTANICAL GAZETTE

SEPTEMBER 1917

ROOT SYSTEMS OF CERTAIN DESERT PLANTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 236

M. S. MARKLE

(WITH THIRTY-THREE FIGURES)

Introduction

Although the aerial parts of plants have long been studied, little was known of the nature of the subterranean parts until the work of CANNON[1] upon the plants of the region about Tucson, Arizona. The supposition had been that in general the roots of desert plants are of great length and deep penetration. The work of CANNON showed that while this is sometimes true, such roots are often of no unusual length and in some cases are very superficial.

Since the soil conditions and the flora of the vicinity of Albuquerque are different from those at Tucson, a study of the roots of plants was undertaken in that vicinity, during the first half of the year 1915. Albuquerque lies in the valley of the Rio Grande, on each side of which are bluffs, leading to an apparently level upland. The mesa on the east rises from an elevation of 200–300 ft. above the valley floor to an elevation of 1200–1500 ft. at the base of the Sandia Mountains 10 miles farther east. This mesa is composed to a great depth entirely of unconsolidated materials, as is shown by a boring of the Water Supply Company 725 ft. deep.[2] It is

[1] CANNON, W. A., The root systems of desert plants. Publ. Carnegie Inst. Wash. no. 131.

[2] BRYAN, K., Geology of the vicinity of Albuquerque. Bull. Univ. N. Mex. no. 5.

concluded from this that previous to the deposition of these beds there was here a deep trough, which other evidence shows to have been the bed of a large river, which existed at a period of greater precipitation and was subsequently filled with stream-borne material. On account of its fluviatile origin the material is extremely variable, being composed of layers of sand, adobe, clay, gravel, boulders, and combinations of these materials, with marked local variations, both horizontally and vertically. On this mesa and the numerous arroyos which dissect its edge grew the plants studied.

One of the principal features of the soil in the habitats described by CANNON is a thick layer of hardpan, or *caliche*, beginning at a depth of about 30 cm. and extending indefinitely. This is so hard as to prevent root penetration, except through cracks. Such layers are common in arid regions, and are formed, according to the opinion of CANNON and others, through the concentration of salts left by the evaporation of ground water gradually ascending by capillarity. Rainfall dissolves these materials, carrying them downward. These two processes result in the formation of a gradually increasing zone of precipitation. In the Albuquerque region this zone is very poorly developed, often being noticeable in a fresh exposure only by the presence of a whitish streak or pebbles stained with lime. When dry, such soil becomes very hard, and it is evident from the appearance of roots entering it that it offers considerable resistance to root penetration, but does not prevent it. When wet the hardpan is soft and easily penetrable. Under natural conditions, however, it is generally very dry.

The Albuquerque region is even more arid than that at Tucson, an average for 10 years giving a precipitation of 7.44 in., as compared with an average of 11.17 for Tucson. Much of this small amount is lost by run-off, since most of the precipitation occurs as torrential summer rains. Table I shows the localization of the rains in the summer months. The marked deviations from the average that are characteristic of individual years are shown by the precipitation during the time of this study in 1915. The lower temperature and the smaller amount of precipitation in the winter

months prevent the growth of the winter annuals so characteristic of the Tucson region.

TABLE I

RAINFALL

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Tucson.....	0.79	0.90	0.77	0.27	0.14	0.26	2.46	2.66	1.16	0.64	0.81	1.00	11.17
Albuquerque, average.....	0.48	0.33	0.22	0.26	0.69	0.35	1.43	1.07	1.70	0.77	0.46	31	7.44
Albuquerque, 1915.....	0.68	0.56	0.51	2.05	0.00	0.00	....	....	....	....	....	....	.....

TEMPERATURE

	1893	1894	1895	1896	1897	1898	1899	1900	1901	1902
Absolute minimum ...	11	0	10	13	2	0	1	9	4	12
Absolute maximum...	98	95	95	100	95	104	104	101	99	100

EVAPORATION FROM A FREE WATER SURFACE

Jan.	Feb.	March	April	May	June	July	August	Sept.	October	Nov.	Dec.
2.04	2.63	6.17	6.82	10.08	12.63	11.78	10.21	8.00	4.38	1.73	1.40

The data for Tucson are given by COVILLE and MACDOUGAL[3] and those for Albuquerque by MAGNUSSON.[4]

A series of determinations of soil moisture was begun, but it was soon found that such data are of little value, since on account of the fact that the soil is composed of stream-borne material, it is subject to extreme local variations, even within the habitat of a single plant, as is shown in the descriptions of the habitats of most of the plants given in this paper. Samples of soil from different levels in the habitat of *Atriplex canescens* showed the following variations in moisture content, the percentages being based upon the dry weight of the soil. Coarse gravel at a depth of 1 ft., 4 per cent; fine sand at 2.5 ft., 10 per cent; hardpan at 4 ft., 3 per cent. Since the precipitation during the time of this study was

[3] COVILLE, F. V., and MacDougal, D. T., Desert botanical laboratory of the Carnegie Institution. Publ. Carnegie Inst. Wash. no. 6.

[4] MAGNUSSON, C. E., Bull. Univ. N. Mex. no. 5.

several times the normal amount, the figures would have had even less value than usual. Similar variations in water holding capacity and wilting coefficient would result from the lack of uniformity in the soil.

On account of climatic differences, the flora is very different from that of the Tucson region. The larger cacti are absent here, all being low forms, excepting *Opuntia arborescens*. No tree is found on the mesa or its arroyos, and the bushes, except *Chilopsis saligna*, are seldom more than 5 ft. in height. The period of greatest growth follows the rainy season, whenever it may occur. There are no winter annuals here, the corresponding forms being either biennials or summer annuals. The annual plants are greatly in the minority, the most conspicuous part of the flora being composed of perennial herbs.

The principal plant associations occurring within the area studied are as follows.

1. The *Bouteloua* association, characterized by the grama and other grasses and formerly occupying the entire mesa, but now much invaded by ruderals, such as *Gutierrezia Sarothrae* and *Salsola*.

2. The *Dysodia-Ephedra* association, dominated by *Ephedra trifurca* and *Dysodia acerosum*. The majority of the plants have reduced aerial parts and a large root system. The association occupies the top and the upper portion of the sides of the gravelly ridges between the arroyos, where exposure and run-off are maximum. The soil is often pure gravel and the surface is generally a mosaic of pebbles.

3. The *Chrysothamnus* association, dominated by *Chrysothamnus Bigelovii* and occupying the lower parts of the sides of the arroyos. The soil is generally adobe, often with much sand and gravel.

4. The *Fallugia* association, dominated by *Fallugia paradoxa* and forming a narrow fringe along the beds of arroyos, which are generally covered with loose sand and gravel.

Method of work

Annuals, biennials, and some of the smaller perennials were removed from the ground and photographed. On account of the difficulty of obtaining the delicate ultimate parts of the roots,

many are necessarily incomplete. It was found possible to photograph some of the larger perennials *in situ*, but in general it was found much more satisfactory to make accurate diagrams of the horizontal and vertical extensions of the root systems on paper metrically ruled in squares. The diagrams appear here drawn to a scale of 1:20, except figs. 25 and 26. While in general only the roots lying in or near a particular plane are represented, it was generally found possible without much distortion to include the most important part of each root system in both the horizontal and vertical diagrams. Roots that for some reason were not followed to the end are terminated in the diagrams by a broken line. Roots turning to a direction at right angles to the plane of the diagram end in a dot.

CANNON divides root systems into 3 types: (1) a generalized type, in which there is a well balanced development of both tap and lateral roots; (2) a specialized form, in which the tap root is much the more prominent; and (3) a second specialized form, characterized by a relatively better development of the lateral roots. This classification is used in the present paper.

Description of root sytems

ANNUALS AND BIENNIALS

Biscutella Wislizeni.—This plant is common in sandy situations on the mesa and in the arroyos. The root system consists of a relatively short tap root, with many strongly developed laterals extending horizontally rather near the surface of the soil. Some of them usually exceed the tap root in length. The specimen shown in fig. 1 grew in a sandy arroyo bed and was about 10 in. in height.

Phacelia corrugata.—This plant is common in a number of associations. It generally occurs as an annual, although specimens in favorable situations may start in the fall and form rosettes which survive the winter. The leaf structure shows almost no xerophytic characteristics, there being only one layer of palisades, large air spaces, and a thin epidermal wall. Considerable variation of the root system occurs under different soil conditions. The plant

shown in fig. 2 grew in a moist situation, where the water of an arroyo was impounded by a dam. The plant is in its early spring condition, the rosette having survived the winter. The root system is of the generalized type. The laterals near the surface are especially well developed, sometimes exceeding the tap root in length. The specimen shown in fig. 3 is from a dry, gravelly ridge in the *Dysodia-Ephedra* association. The impoverished condition of the plant is shown by the weak development of both root and shoot. Here the tap root is relatively the more important.

FIG. 1.—*Biscutella Wislizeni*

Allocarya crassisepala.—This is one of the most common annuals of the mesa and arroyos and is a ruderal in a number of associations. The plants vary very greatly with the soil conditions in both root and shoot. The plant shown in fig. 4 grew in moist soil in the bottom of an arroyo and bore numerous prostrate branches. The root system was superficial and consisted of a short tap root which soon became horizontal, and a number of long, branched laterals arising about an inch below the surface of the soil. The plant shown in fig. 5 grew in dry soil and had a tap root relatively well developed and vertical, with smaller and less numerous laterals.

Sisymbrium canescens.—This plant is common in a number of associations. It makes a quick growth and maturity after a period of rain. The root system is very small in proportion to the shoot and consists of a tap root with a number of small laterals.

Linum rigidum.—This plant is characteristic of the *Dysodia-Ephedra* association. Both root and shoot are much reduced. The root system in the plant shown in fig. 7 consisted of a tap root about 5 in. long and a few short laterals with almost no fine ultimate branches.

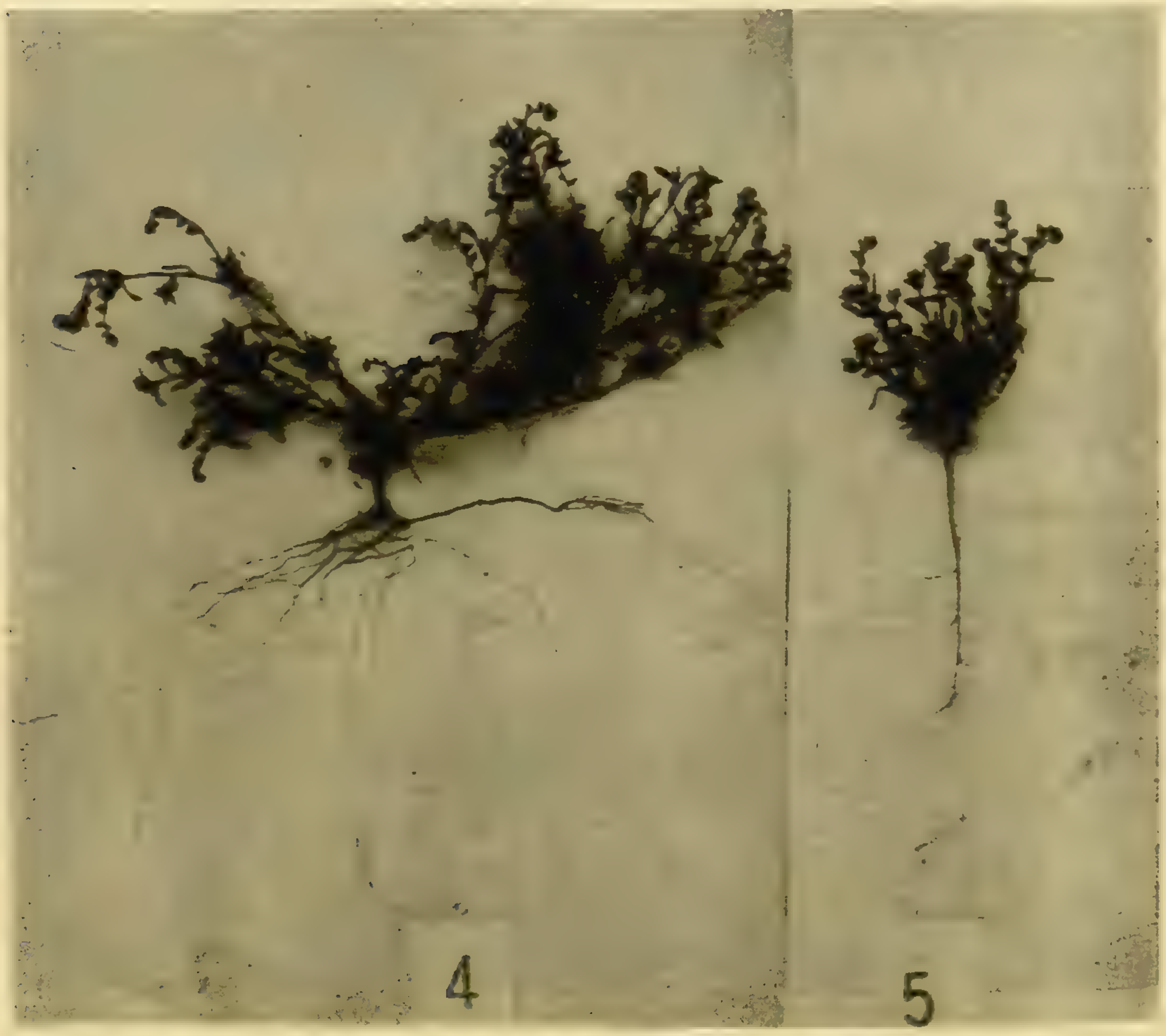
FIGS. 2, 3.—Fig. 2, *Phacelia corrugata* from moist habitat; fig. 3, *P. corrugata* from dry habitat.

PERENNIAL HERBS

Cymopterus Fendleri.—This plant is exceedingly common on the mesa and the ridges between the arroyos. It is the earliest plant to begin growth and to blossom in the spring. The leaves are in the form of a loose rosette and are xerophytic in structure. The root system is characterized by a thick, fleshy tap root which occasionally bears one or two fleshy laterals. In the growing season there appear numerous slender, white, absorptive roots

which later are deciduous. These always break off upon removal from the soil and do not appear in the figure.

Rumex hymenosepalus.—This plant is common in the more mesophytic places on the mesa, especially in broad, shallow arroyos. The rosette of broad, thick leaves appears very early in the spring and is soon followed by a spike of flowers. The root is very large



FIGS. 4, 5.—Fig. 4, *Allocarya crassisepala* from moist habitat; fig. 5, *A. crassisepala* from dry habitat.

and fleshy. Young roots are constantly being formed as the oldest decay. The irregular projections at the top of the root shown in fig. 9 represent 10 or 11 crowns of former years. The youngest roots bear short laterals, but the older ones are generally without them. It is interesting to note that of the plants studied the three having the most prominent storage organs in the way of thickened roots all grow in situations more mesophytic than the average.

Rumex is common in the arroyos on the mesa; *Cucurbita foetidissima* occurs most abundantly along the banks of irrigation ditches in the valley; *Berlandiera lyrata* is confined almost entirely to the sides of arroyo beds. Thus it appears that the plants having this "adaptation" to an arid environment are in less need of it than most of the plants of the region.

FIGS. 6, 7.—Fig. 6, *Sisymbrium canescens;* fig. 7, *Linum rigidum*

Astragalus diphysus and *A. mollissimus.*—These are common evergreen plants of the mesa. The root systems are similar and are characterized by prominent tap roots with a few large and several small laterals, which are generally deeply placed. The root tubercles are small and not numerous. A plant of *A. mollissimus* is shown in fig. 10.

Solanum eleagnifolium.—This plant is very characteristic of sandy situations and the rapidly eroding sides of arroyos. The

plant shown in fig. 11 grew in the latter situation. The upper 12 in. of soil was sandy adobe, followed by 10 in. of clayey adobe with some gravel. Below this was a layer of loose gravel about 2 in. in thickness, under which was fine sand to an unknown depth. The plant was 18 in. in height. The root system was of the specialized type with strongly developed tap root. There were a few well developed laterals, two of which arose at the junction of the layers of sandy and clayey adobe. Upon reaching the layer of loose gravel, one of these turned abruptly and proceeded horizontally in the gravel layer, possibly on account of the greater ease of penetration. Another took a rather tortuous course downward and was lost at a depth of 65 in., below the level of the bottom of the arroyo. This root had a length of 72 in., and since its diameter at the broken end was 3 mm., its total length was undoubtedly much greater. Numerous small laterals arose in the upper 12 in. of soil.

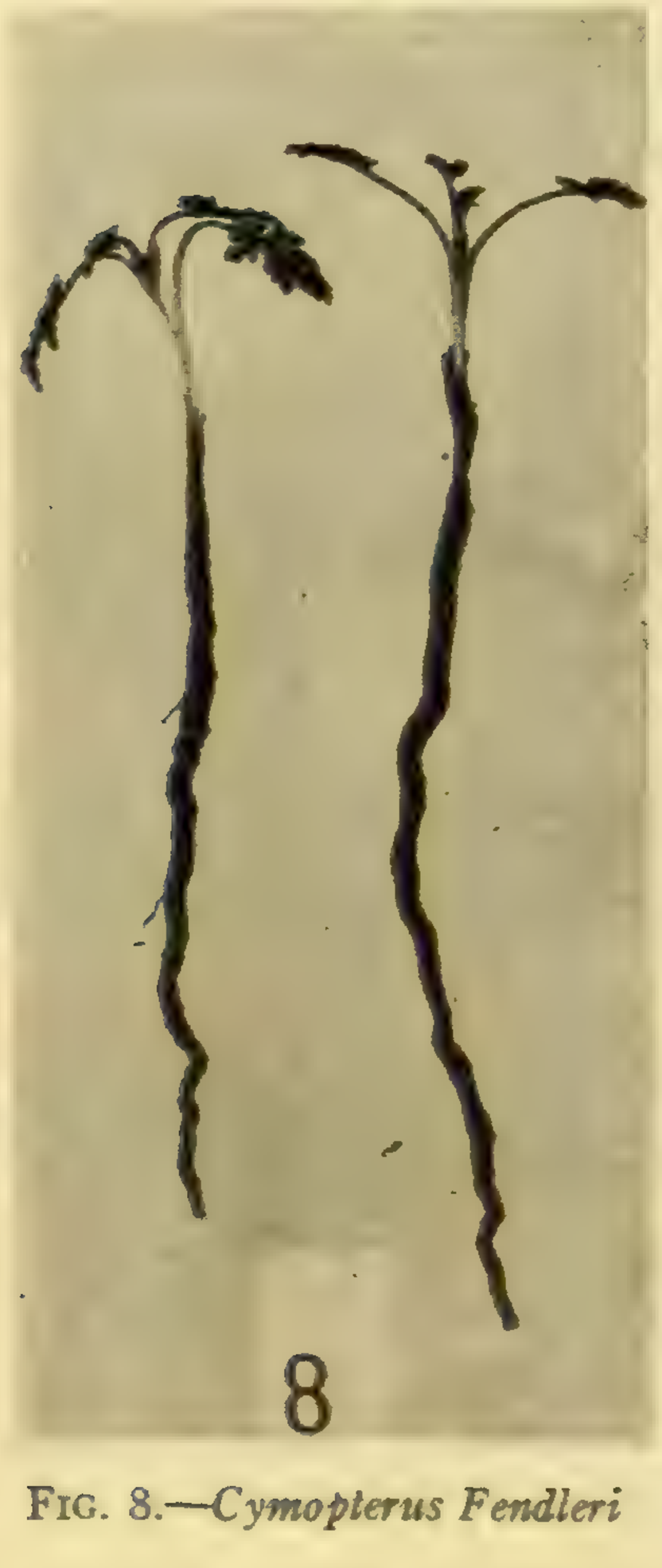


FIG. 8.—*Cymopterus Fendleri*

Cucurbita foetidissima.—This perennial herbaceous vine is common along irrigation ditches in the valley and less so along the sides of arroyo beds. The root is extremely thick and fleshy and is surmounted by an underground stem 6 in. in length. The main root of the plant studied was about 3.5 in. in diameter at the top and extended to a depth of 20 in., gradually becoming horizontal and forking several times after reaching a length of 36 in. The main root bore only one small lateral (fig. 12).

Pachylophus hirsutus.—This plant is a rosette in habit and is found in the driest and most exposed slopes of the gravelly ridges of the *Dysodia-Ephedra* association. The leaves are hairy and rather thick and succulent. The root system is fleshy and of

irregular form, without evident differentiation into tap root and laterals. The main root often proceeds horizontally and is little larger than the minor roots. The specimen shown in fig. 13 grew in pure gravel.

Euphorbia sp.—This small, prostrate plant grows on the sides of arroyo beds. The root system has much the same general form

FIGS. 9, 10.—Fig. 9, *Rumex hymenosepalus;* fig. 10, *Astragalus mollissimus*

as that of *Sphaeralcea*, but all the roots are slender, brown, and fibrous. The identity of the tap root is lost a short distance below the surface. The slender ultimate branches are very numerous. The root system is not deep, but very thoroughly permeates a limited amount of soil (fig. 14).

Sphaeralcea cuspidata.—This plant is very common in the *Bouteloua* and *Dysodia-Ephedra* associations. The plant shown in

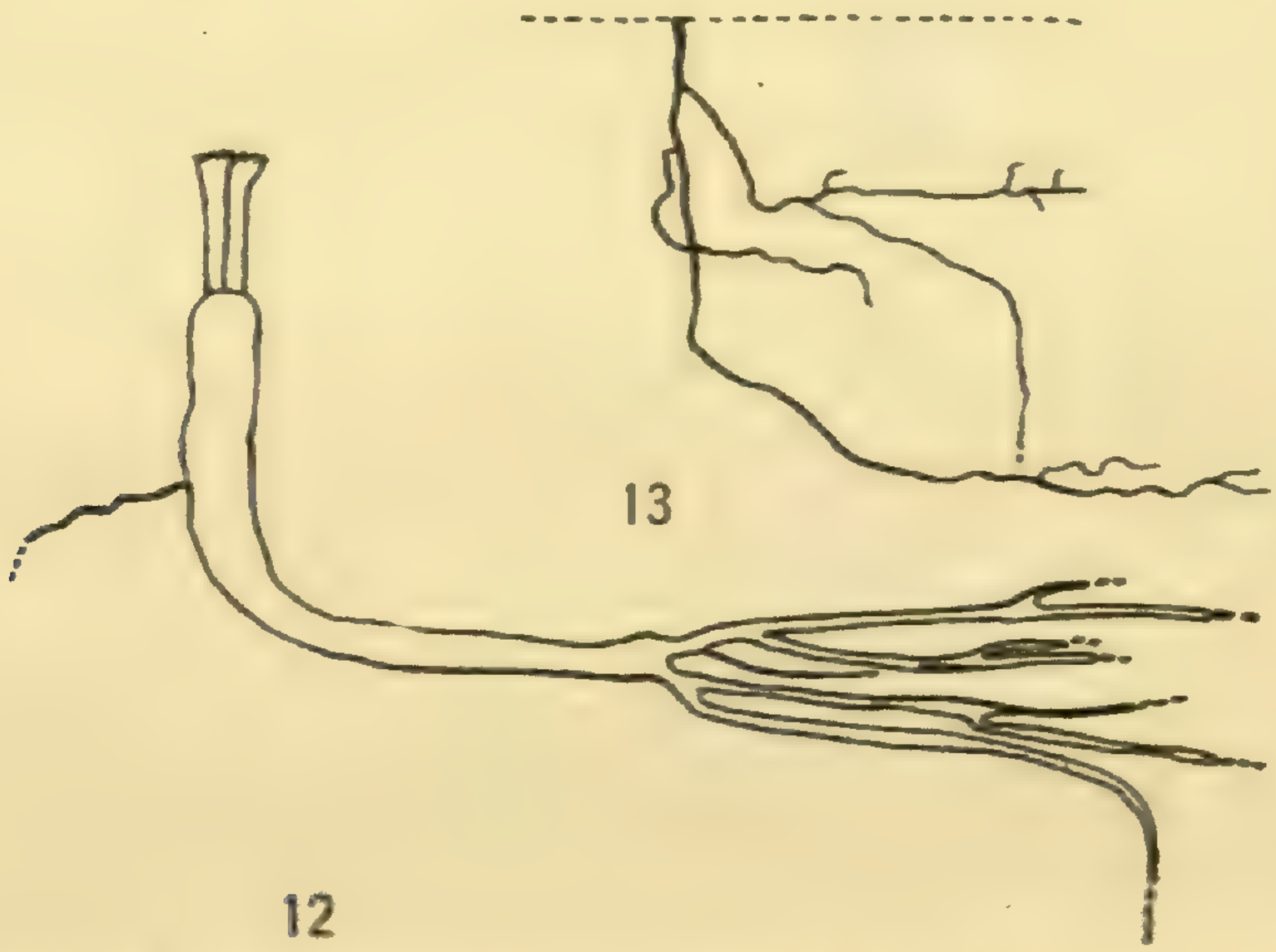
fig. 15 grew in sandy soil on the mesa. The root system is characterized by a tap root which is poorly differentiated or even absent, and very prominent laterals. The remains of the crowns of several years are shown. When the plant grows in an unstable situation, such as the rapidly eroding side of an arroyo, vegetative reproduction from the roots occurs very commonly, enabling the plant to maintain a foothold.

FIG. 11.—Vertical extension of root system of *Solanum eleagnifolium*.

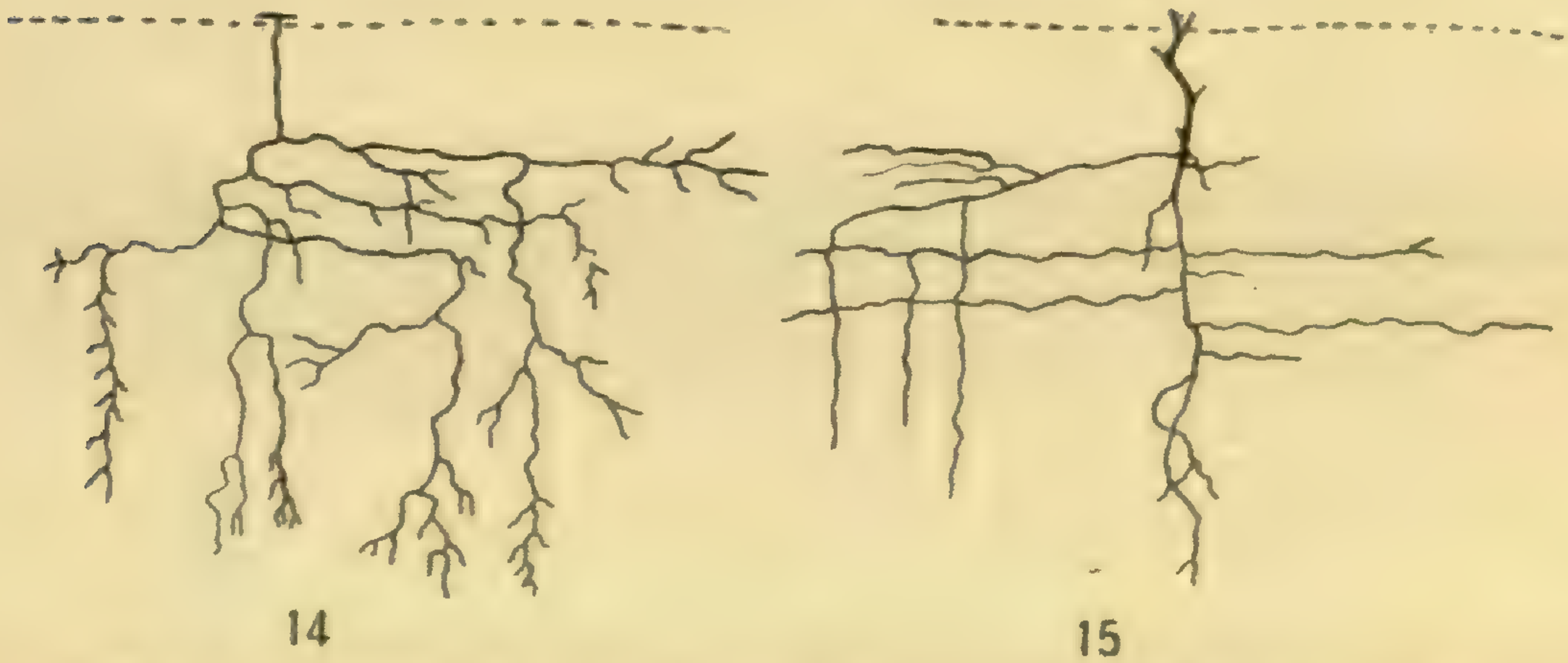
Berlandiera lyrata.—This plant is confined almost entirely to the sides of arroyo beds. The root system has a stout tap root with very few laterals. The group of laterals near the surface of the ground in so many plants of the region is absent here. The entire root system is thick and fleshy and the upper portion is swollen to the thickness of an inch. Plant *A*, fig. 16, grew about 1 ft. above the bed of an arroyo. The tap root divided into two horizontal branches slightly below the level of the arroyo bed. Plant *B* grew about 4 ft. above the bed of an arroyo and bore no extensive laterals until it reached the level of the bed of the arroyo, where it branched freely. The length of the tap root is apparently determined by the distance to the layer of moister soil on a level with the arroyo bed.

Gaura coccinea.—This perennial herb is very common on eroding arroyo sides and other disturbed situations. The root system belongs to the specialized type with prominent tap root. The length of the tap root is apparently determined by the distance of the plant above the arroyo bed. There are few laterals, most of

the absorption probably being done by the ultimate branches of the tap root. Vegetative reproduction from the roots is common (fig. 17).



FIGS. 12, 13.—Fig. 12, vertical extension of root system of *Cucurbita foetidissima*; fig. 13, vertical extension of root system of *Pachylophus hirsutus*.



FIGS. 14, 15.—Fig. 14, vertical extension of root system of *Euphorbia* sp.; fig. 15, vertical extension of root system of *Sphaeralcea cuspidata*.

SHRUBS

Parosela formosa.—This low, much branched shrub is confined almost entirely to the sides of arroyo beds in the *Fallugia* association. The leaves are very small and xerophytic in structure. Several root systems were dug up and found to belong to the specialized type with prominent laterals, resembling somewhat the

cactus type. In some specimens no tap root could be distinguished, although a better development of the tap root was found in plants

FIGS. 16, 17.—Fig. 16, vertical extension of plants of *Berlandiera lyrata: A*, growing 1 ft. above arroyo bed; *B*, growing 4 ft. above arroyo bed; fig. 17, vertical extension of root system of *Gaura coccinea*.

FIG. 18.—Vertical and horizontal extensions of root systems of *Parosela formosa*

growing higher above the arroyo bed. The plant shown in fig. 18 grew on the edge of a gravelly arroyo bed 6 ft. wide. The specimen

FIG. 19.—Vertical and horizontal extensions of root system of *Artemisia tridentata*

FIG. 20.—Root system of *Ephedra trifurca*

was 28 in. in height. The tap root was weak, being exceeded in diameter by several of the laterals. The laterals were numerous and arose just below the ground and proceeded horizontally 2 or 3 in. below the surface, most of them beneath the bed of the arroyo. The ends of several of them dipped abruptly downward. This type of root is rare in the region. The root system of *Parosela scoparia*, which grows in sand, was found to be similar, but more deeply placed.

FIG. 21.—Root system of *Dysodia acerosum*

Artemisia tridentata.—This plant grows along the sides of arroyos in the *Chrysothamnus* association. Well developed specimens are rare, since the plant is freely eaten by grazing animals. The specimen shown in fig. 19 grew in soil the upper 10 in. of which was adobe, overlying 12 in. of coarse gravel and pebbles, with adobe below this to an unknown depth. The tap root was well developed, but the laterals near the surface were extremely prominent. These were of two types: numerous short ones in the upper 12 in. of soil, and a few very long ones which arose from the upper 6 in. of the tap root. The latter proceeded horizontally 3–4 in. below the surface of the soil and reached a length of 20–40 in. There was a tendency for the ends of these roots to turn downward, as in *Parosela*.

Ephedra trifurca.—This is one of the dominant species of the *Dysodia-Ephedra* association. Investigation of a number of

specimens showed a considerable variation in the root system, which in general has a good development of both tap and lateral roots. The plant shown in fig. 20 grew in adobe soil about 2 ft. above the bottom of an arroyo and had prominent laterals and a stout but rapidly tapering tap root. Below the part shown in the photograph, two large laterals were given off, below which the tap root was insignificant. Another specimen growing in adobe soil 10 ft. above the bottom of an arroyo and exposed by erosion showed a relatively much greater development of the tap root. Several laterals, the largest half an inch in diameter, were given off in the upper 2 ft. of soil. Three small laterals occurred 3 ft. below the surface. The tap root proceeded somewhat tortuously downward to a depth of at least 11 ft., a little below the level of the arroyo bed, where a large lateral arose. Below this the tap root had a diameter of 5 mm. and was not followed farther. A third specimen grew on a hill and was exposed by the removal of gravel. The plant grew in a soil composed of boulders up to 8 in. in diameter, the interstices of which were filled with sand. The root system was essentially similar to the second specimen described. The cause of the variation in the length of the tap root apparently is not the character of the soil,

FIG. 22.—Root system of *Chrysothamnus Bigelovii*

but the height of the plant above the nearest arroyo. Even though there is a stream in the arroyo only a few hours each year, there is probably a layer of moister soil on a level with the bottom of the arroyo, on account of a slow creep of ground water toward the arroyo and the conservation of the moisture by the dry sand covering it.

Dysodia acerosum.—The habitat of this plant is the same as that of *Ephedra*. The aerial parts of the plant form a compact, much-branched tuft. The leaves are needle-like. The individual photographed grew in sandy adobe with large pebbles (fig. 21). The plant had a stout tap root with a few large laterals arising close together a short distance below the surface of the soil. The tap root shown measures 39 in., but it was probably several inches longer. Both tap and lateral roots bore numerous fine branches.

FIG. 23.—Root system of *Opuntia fragilis*

This species probably has the largest root system in proportion to the size of the aerial parts of any of the plants of the region.

Chrysothamnus Bigelovii.—This is the dominant plant in an association characteristic of the lower parts of the sides of arroyos. The principal photosynthetic work is done by the almost leafless green stems. The root system is of the generalized type. Fig. 22 shows only a part of the root system of a rather young plant. Later excavation showed laterals up to 90 and 100 in. in length and a tap root about 100 in. long. The laterals are usually of small diameter

and taper very slightly and bear numerous small lateral branches, especially near their distal ends. Older individuals probably have root systems more extensive than that of any other plant of the arroyos or mesa.

Opuntia fragilis.—This is the smallest and most common cactus of the mesa, where large colonies form mounds of sand or adobe. The root system is very superficial and consists of one or two main roots with numerous small lateral branches (fig. 23).

Opuntia arborescens.—This is the only large cactus found in the region. It is characteristic of the pine-cedar association of the mountains and occurs sparingly on the mesa. The specimen shown in figs. 24 and 25 grew in the latter situation and was only 2.5 ft. in height. The root system is similar to the type described by CANNON for the larger forms occurring near Tucson. There is a sharp differentiation of absorptive and anchorage roots. The former are long and thin and occur within an inch or two of the surface; the latter are short and thick and deeply placed. The longest absorptive root had a length of 93 in.; the longest anchorage root a length of 30 in. The absorptive roots have many fine branches, especially near the ends.

FIG. 24.—Anchorage roots of *Opuntia arborescens*, vertical extension.

Opuntia camanchica.—This is the common prickly pear of the mesa and arroyos. The specimen shown in fig. 26 occurred in the *Dysodia-Ephedra* association in gravelly sand with small boulders. The plant had been formed vegetatively from a fallen segment which had become buried. The roots had originated from the pulvini and the proximal 2 inches of each was tuberous. The root system conforms to the usual superficial type described by CANNON for the smaller cacti, except for the presence of one thick, deeply placed root. The plant is usually several joints in height, so that

FIG. 25.—Absorptive roots of *Opuntia arborescens*, horizontal extension

especially in a strong wind there is considerable strain on the lower joint. The presence of the thicker, more deeply placed root may show a tendency toward the sharp differentiation of anchorage and absorptive roots so well shown by *Opuntia arborescens*.

Mamillaria Grahami.—This little cactus occurs sparingly in the driest parts of the *Dysodia-Ephedra* association. The root system differs from the usual cactus type in having a short but well marked tap root which bears many short and a few longer laterals.

Yucca glauca.—This plant is very common along arroyos on the mesa and in sandy soil. The plants generally grow in clumps

formed by vegetative multiplication. The root system consists of a thick, branched, horizontal portion bearing numerous laterals quite uniformly about 3 mm. in diameter. Those measured showed lengths of 5, 6, 7, and 24 in. The main root is usually about 2 in. in diameter and very succulent. It evidently functions as a storage organ.

FIG. 26.—Vertical and horizontal extensions of root system of *Opuntia camanchica*

Eriogonum effusum.—This low shrub is characteristic of the edges of arroyo beds. The root system is of the generalized type. The plant shown in fig. 28 grew about 4 ft. above the bottom of an arroyo. The composition of the soil was as follows: upper 32 in., coarse sand and gravel; 10 in. of moist sand; dry gravel to an unknown depth. Several prominent laterals penetrated the sand and gravel layer. Two of the largest laterals occurred in the layer of moist sand. Another specimen, which grew about 10 ft. above the bed of an arroyo, had a tap root 80 in. long with the laterals

confined almost entirely to the space between the 16 and 24 in. depths. The effect of the position of the plant with reference to the arroyo bed is shown here.

Gutierrezia Sarothrae.—This semi-evergreen shrub is a common ruderal in many associations of mesa, mountain, and valley, but especially on the mesa, where grazing has been a greater disturbing factor. The plant shown in the photograph grew near the bottom of an arroyo and had a root system of the generalized type. The

FIG. 27.—*Yucca glauca*

plant shown in the diagrams was a small specimen 8 in. in height and grew near the edge of the steep bank of an arroyo bed. The tap root was especially well developed and extended vertically to a depth of 44 in., where it reached the level of the bottom of the arroyo. Here the tap root turned and extended out under the bed of the arroyo a distance of 100 in., branching freely. The horizontal part of the root was within 2 in. of the surface and bore numerous fine absorptive roots. It is evident that the unusual development of this root system is a response to moisture conditions, and it is doubtless to this ability to respond to varying conditions that

the plant owes its success as a ruderal in so many associations (figs. 29, 30).

Atriplex canescens.—This evergreen shrub is common on the fans at the mouths of arroyos and less so along the sides of the smaller arroyos. A small plant 18 in. in height and growing in a small arroyo was selected for excavation. The upper 15 in. of the soil was sandy adobe, underlaid by 32 in. of coarse sand and gravel and 15 in. of hardpan. The plant had a strong tap root which forked at a depth of 32 in. One branch continued vertically downward and penetrated the hardpan layer. The other branch

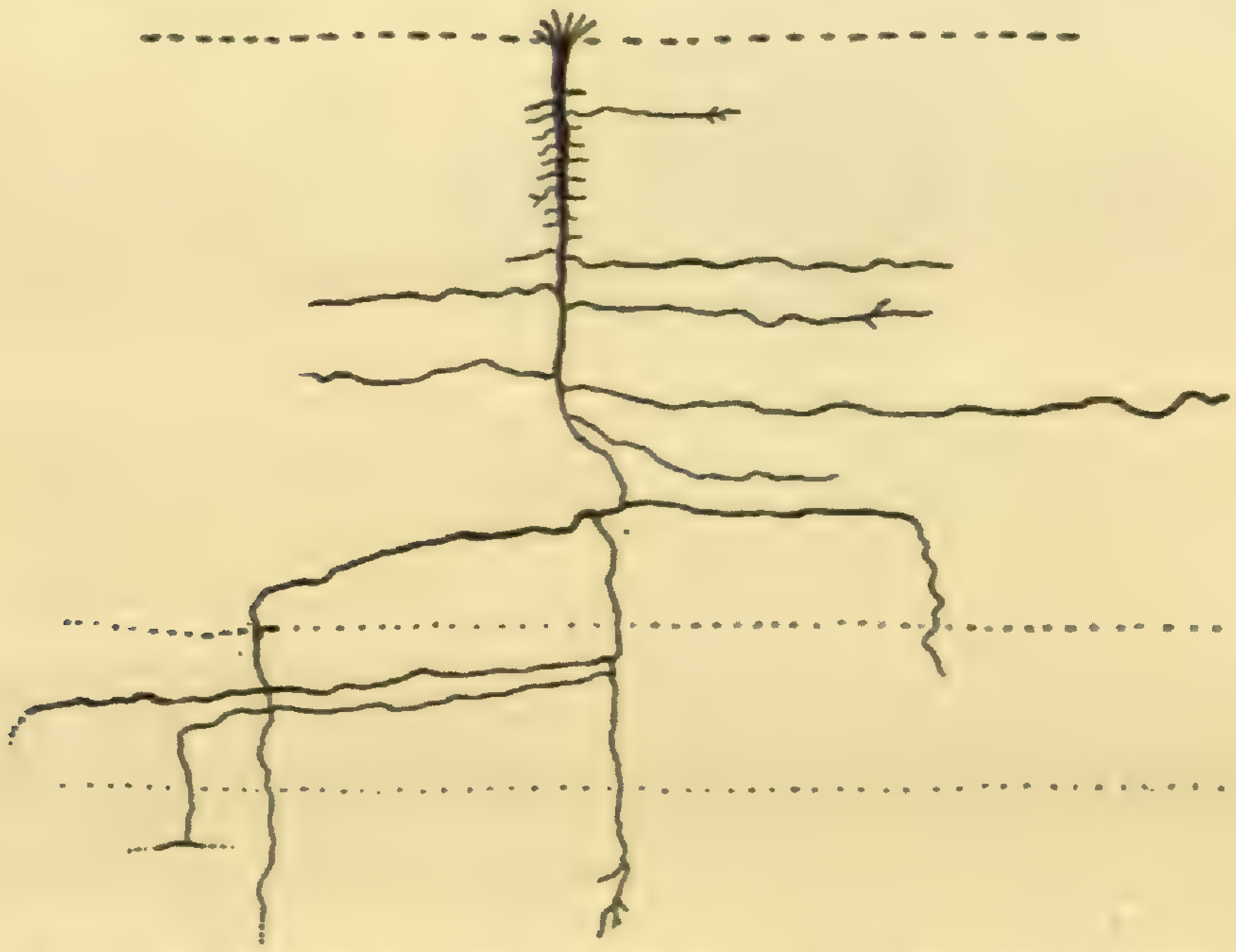


FIG. 28.—Vertical extension of root system of *Eriogonum effusum*

again forked and the subdivisions followed a tortuous course on top of the hardpan layer, twisting in every direction. One finally penetrated it diagonally. The effect of the hardpan in resisting root penetration was evident from the twisted character of the roots (figs. 31, 32, 33).

Lycium pallidum.—This solanaceous shrub is one of the most common plants along the sides of arroyos, especially where erosion is active. The root system is so peculiar that a large number of plants was examined. Unlike the roots of most of the plants of arroyo sides, the root system of *Lycium* is almost entirely horizontal.

A few laterals may extend upward. The main root of a specimen 18 in. in height was followed along the face of a steep bank for a distance of 15 ft., at which point the root was a quarter of an inch in diameter. The superficial character of the root system makes possible the vegetative multiplication by which the plant maintains itself in its unstable habitat. Erosion exposes the roots, which put forth new shoots.

FIG. 29.—*Gutierrezia Sarothrae* from near bottom of arroyo.

Discussion

On account of the fact that here, where the soil is of fluviatile origin, the conditions to which roots are exposed vary so much, even within the habitat of a single plant, the causes of any variations in the root systems are difficult to determine. Variations are common, but they may be due to one or more of a large number of soil factors, such as the composition of the soil, its penetrability, its alkalinity, its wilting coefficient, etc. The problem of the causes of root variation is one to be attacked under laboratory conditions, in which one factor can be varied at a time.

Observation, however, made apparent the effect of at least two factors, penetrability and water content. Roots were often seen to turn abruptly from a layer of clay or adobe and follow a thin layer of sand or fine gravel containing much less water but more easily penetrable. This is illustrated by the root system of *Solanum*

eleagnifolium, shown in fig. 11. A layer of soil difficult of penetration may cause much distortion of roots entering it, as seen in the diagram illustrating the roots of *Atriplex canescens*.

The most striking instance of the effect of a variation in the water content of the soil is shown in the roots of plants growing along arroyos. Nearly all of these are characterized by long tap roots, the length of which apparently is determined by the height of the base of the plant above the moister soil below the level of the

FIG. 30.—Vertical and horizontal extensions of root system of *Gutierrezia Sarothrae* from top of arroyo side.

arroyo bed. These variations are shown in the diagrams of the roots of *Ephedra*, *Gutierrezia*, *Berlandiera*, and others.

To which of the three general types of root systems that of a given individual belongs seems to be largely predetermined, a constant character of the species; but wide variations within the types, affecting the size and proportions of the root system, may occur through the influence of soil factors.

CANNON (*loc. cit.*) has pointed out the relation between the type of root system and the distribution of a species. In general, he finds that the species with root systems of the general type have

the widest distribution, while those with the specialized types are confined to peculiar habitats.

Gutierrezia Sarothrae, which has a generalized root system, is very widely distributed in primitive growths and as a ruderal. A number of species are confined here to the sides of arroyo beds and are characterized by prominent tap roots. *Lycium pallidum* has prominent horizontal roots and is confined almost entirely to rapidly eroding banks.

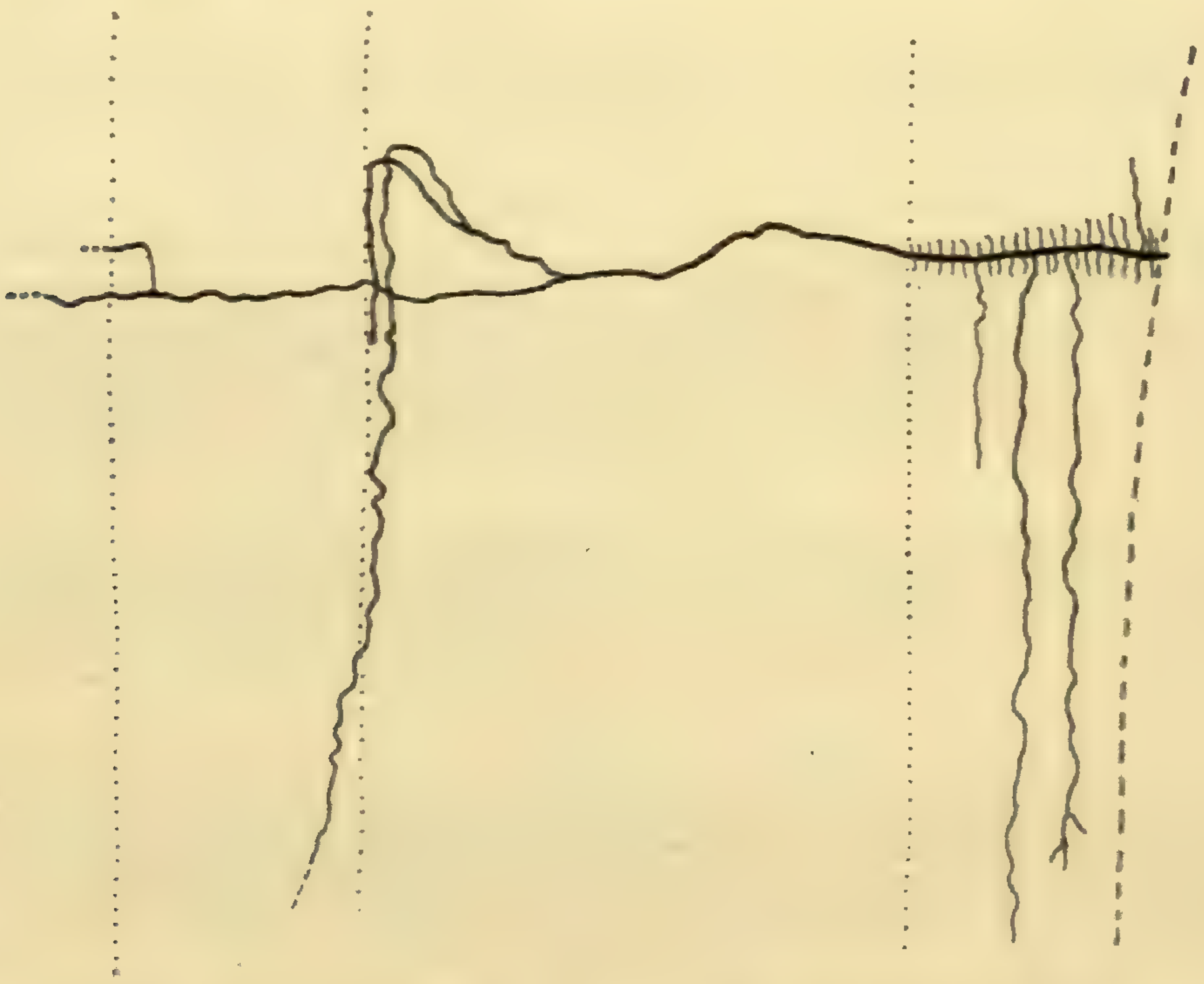


FIG. 31.—Vertical extension of root system of *Atriplex canescens*

Contrary to what might logically be expected, the species having the most fleshy roots grow in situations better watered than the average. *Cucurbita foetidissima* grows near irrigation ditches and along arroyos; *Rumex hymenosepalus* occurs in the broad arroyos crossing the mesa; *Berlandiera* is confined almost entirely to the sides of arroyo beds; *Yucca* occurs more commonly along arroyos than on the level mesa.

A knowledge of the interrelations of the roots of the plants of an association doubtless would throw light on many ecological questions. In a mesophytic association especially, the development of layers of the aerial parts of plants with reference to light

is very prominent. A comparable adjustment of the roots of plants with reference to soil moisture probably exists in all types of associations, but especially in arid habitats soil moisture is a limiting factor and root competition is more severe. Observations of the distribution of the roots of some of the associations were made on rapidly eroding arroyo banks and sand and gravel pits.

In the *Bouteloua* association, the most superficial layer of roots is that formed by the grasses, principal among which are *Bouteloua eriopoda* and *Hilaria Jamesii*. Most of the roots of these grasses occupy the upper 2 in. of soil, although some of them go much deeper. The roots of *Hilaria* are very tough and woody and reach a length of 6 ft. or more. The thorough permeation of the upper

FIGS. 32, 33.—Fig. 32, horizontal extension of root system of *Atriplex canescens* at depth of 44 in.; fig. 33, horizontal extension of superficial roots of *Atriplex canescens*.

layers of the soil by the roots of these grasses no doubt accounts for the relatively pure growth of grasses in this association. They so thoroughly remove the water from the superficial layer that seedlings of deeper rooted plants perish before the lower, moister layers are penetrated. Over large areas, overgrazing has destroyed most of the grass, giving opportunity for the entrance of such ruderals as *Gutierrezia* and *Salsola*.

In the *Dysodia-Ephedra* association, the upper layer of roots is made up of the roots of annuals, cacti, and grasses, such as *Bouteloua eriopoda*, *Hilaria Jamesii*, *Munroa squarrosa*, and *Pappophorum Wrightii*. These are very superficial and interfere little with the roots of the other plants of the association, as the grasses nowhere occupy large areas and the germination of seedlings is not prevented.

A second region of root penetration is occupied by the relatively superficial laterals so common among the plants of the region. These in general are more deeply placed than the roots of the grasses and annuals. *Dysodia acerosum*, *Aplopappus*, *Euphorbia*, and *Hymenopappus* are the principal plants.

A third layer of roots is made up of the lateral roots of *Ephedra* and the deeper parts of the root systems of *Dysodia*, *Allocarya Jamesii*, *Pachylophus hirsutus*, *Melampodium*, and others.

The fourth layer probably does not always occur, but near an arroyo it may contain more roots than any except the superficial layer. Here occur the ultimate branches of the tap root of *Ephedra*, *Gaura coccinea*, *Berlandiera lyrata*, *Stephanomeria runcinata*, and others.

The zonation of the roots reduces competition and permits the growth of a larger number of species. The root systems of the two dominant plants compete but little, since the principal absorptive roots of *Dysodia* occur in the third layer and those of *Ephedra* in the third and fourth layers. This no doubt accounts for the joint dominance of the two plants.

Summary

The region at Albuquerque differs from that of Tucson in having about two-thirds as much rainfall and much lower winter temperatures. The soil of the mesa is fluviatile in origin and very diverse in composition. The hardpan layer prominent at Tucson is not well developed. The winter annuals and the larger shrubs and cacti are absent. Most of the plants are perennial herbs.

The root systems generally penetrate rather deeply, but often have prominent laterals near the surface of the soil. The cacti and a few of the shrubs have a very superficial root system. The larger cacti show a differentiation into anchorage and absorptive roots. The plants of arroyo sides have prominent tap roots varying in length with the height of the plant above the bottom of the arroyo. Storage roots are uncommon and are more characteristic of the moister situations. Vegetative reproduction from roots is common in the plants of unstable soil.

While the causes of root variation can be accurately determined only under laboratory conditions, two factors exert a very evident influence, variation in the penetrability of the soil and in its moisture content.

The roots of the plants of an association are grouped into rather definite layers, so that root competition is lessened. The composition of an association is probably determined largely by root competition.

The writer wishes to express his appreciation of the assistance of Professor HENRY C. COWLES during the course of this investigation.

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DEVELOPMENT OF SOME SPECIES OF PHOLIOTA

W. H. Sawyer, Jr.

(WITH PLATES XVI–XX)

The taxonomy of the Agaricaceae at the present time is based upon characters of the mature plant which in many cases are slight and superficial and of uncertain homology. It is very probable that a knowledge of the origin and method of development of the different structures composing the mature fruit body would aid greatly in determining true relationships among the different genera and species, and it is for this reason that a comparative study of the morphology and development of the basidiocarp is important.

The first serious study in the Agaricaceae of the origin and differentiation of the parts of the young fruit body began over half a century ago, when Hoffmann (**19**), in 1856, briefly described the origin of the hymenium in *Agaricus campestris* and two other species. Four years later Hoffmann (**20**) gave a brief account of the development of several additional species, in all of which the hymenium was exogenous in origin except one, *Marasmius oreades*.

In 1866 DeBary (**13**) studied the development of several species of Agaricaceae, and his work was followed in 1874 by Hartig's (**18**) description of *Armillaria mellea*, Brefeld's (**12**) work upon *Coprinus* in 1877, and in 1889 by Fayod's (**15**) very cursory study of 43 species, with hymenium both exogenous and endogenous in origin. Nothing more was done along this line of research until 1906, when Atkinson (**2**) published a thorough description of the development of *Agaricus campestris*, and the stimulus given by this work has been evidenced during the last 10 years by several publications on the development of different agarics, notably those of Allen (**1**), Beer (**11**), and Fischer (**16**).

The material for the following investigation was collected during the late summer of 1915 in the vicinity of Seventh Lake, in the Adirondack Mountains, New York. The 3 species, *Pholiota squarrosa*, *P. flammans*, and *P. adiposa*, were all growing upon

rotten coniferous wood, presumably *Picea rubra*. Material of all 3 species was very abundant in several different localities, and in each case the young stages selected were identified beyond the possibility of a doubt by mature specimens associated with them. An abundance of material in all stages of growth was fixed in Carnoy's fluid and carried into cedar oil before returning to Ithaca, where it was imbedded, some in paraffin and some in collodion, and sectioned for study.

Pholiota squarrosa

Young fruit bodies, in the stage of development shown in fig. 1, are elliptical or elongate in outline and composed of hyphae loosely interwoven in the basal region, but more compact toward the apex, with some of the threads radiating from the summit. Scattered through the tissue of the fruit bodies are hyphal threads, somewhat straighter and more even in diameter than the ordinary hyphae, which are conspicuous because of their property of taking a very deep stain. These differentiated hyphae are present not only in the youngest basidiocarps, but in successive stages of development, and in all 3 species studied. Their function is unknown, but probably they serve some special purpose in nutrition. Glycogen has been shown to occur in large quantities in many fungi (*Phallus*, et al.) as a reserve food material, utilized during growth, and it may be that these peculiar threads owe their deep-staining properties to the presence of this substance.

DIFFERENTIATION OF STEM FUNDAMENT.—In the fruit body shown in fig. 1 a small, deeply staining area occurs in the central apical part; this is a region of active growth, with hyphae slightly more slender and richer in protoplasm than the other hyphae of the fruit body. This region marks the apex of the stem fundament, and in younger stages of development than the one represented here would in all probability be found to originate in the base of the fruit body, as shown in fig. 25 for *P. flammans*. In this species, as will be described more fully later, the fundament of the stem appears first in the base of the fruit body as a deeply staining area, which by progressive growth and differentiation moves to the apical part (fig. 26). A similar origin of the stem fundament has been

described in *Lepiota cristata* and *L. seminuda* (10), in species of *Cortinarius* (14), and in *Rozites gongylophora* (22).

In further stages of development, the hyphae in the stem fundament, by interstitial growth, form a compact, broadly conical area, whose apex is the dark-stained region and whose sides in median longitudinal sections slope outward at a strong angle (fig. 8). The hyphae pursue a rather uniformly longitudinal direction of growth, and are rich in protoplasm; the peripheral threads, because of this longitudinal arrangement and their deeply staining qualities, delimit the surface of the stem from the enveloping ground tissue, whose hyphae are poor in protoplasmic content and without definite direction.

DIFFERENTIATION OF HYMENOPHORE AND PILEUS PRIMORDIA.—During an early stage in the differentiation of the stem fundament there appears, in median longitudinal sections, in the ground tissue on either side of the apical part of the fundament, a small mass of hyphae, which is readily distinguishable from the surrounding tissue because of the compact nature of the hyphal complex and its property of taking a deep stain (figs. 4, 7). Serial longitudinal sections show that these hyphae occur in a ring around the apex of the stem primordium; they are the earliest evidence of the differentiation of the primordium of the hymenophore. The appearance of the hymenophore primordium differentiates the fundament of the pileus from the stem fundament, although as yet the tissue composing it is very loose and hardly to be distinguished from the surrounding ground tissue. The individual hyphae that make up the hymenophore primordium grow down from this area; at first they are crowded, very rich in protoplasm, and run in every direction, or in some cases may even be wound up into a ball (fig. 6). As the development of the fruit body proceeds, the hyphae grow out of the tangled condition in which they exist in the youngest stages of the hymenophore primordium and take a downward course. By the intercalary growth of new hyphae from above the primordium of the hymenophore becomes more compact and broadens out, keeping pace with the margin of the pileus primordium, which by interstitial and marginal growth is continually moving centrifugally toward the periphery of the fruit body. At first the hyphal threads

in the hymenophore are slender and somewhat pointed; they show a tendency to aggregate themselves at the tips into groups or tufts, with the ends of several hyphae in each tuft, and the different tufts separated by narrow interstices, so that the primordium often presents a rough and jagged appearance in this stage of its development.

BLEMATOGEN.—In the youngest fruit body sectioned (fig. 1) the universal veil consists of hyphae which push up at the apex and turn downward in all directions. There is little doubt that if younger stages had been available for study, a condition would have been found similar to that in the very young fruit bodies of *P. flammans*, where the hyphae in the beginning are loose and radiate from all over the surface of the basidiocarp (fig. 24). In the stage shown here, however, the development has proceeded to a condition where the hyphae of the lateral surface of the fruit body have taken on a direction of growth parallel to the axis of the stem fundament; a central core or strand of hyphal threads in the apex grow upward more rapidly than the surrounding tissue, and by curving backward and downward form a covering, which is the blematogen, over the entire surface of the fruit body. The hyphal cells thus exposed upon the outside become enlarged and many of the outermost ones lose their protoplasmic content and become oval or globose. The hyphae composing the fruit bodies shown in fig. 1 are 3–5 μ in diameter near the base, and in the apical region they are slightly more slender, averaging about 3 μ in thickness, while the hyphae of the blematogen layer are much thicker, being 8–15 μ in diameter. The condition existing here is somewhat similar to the origin of the blematogen in *Coprinus lagopus* (12), as described and figured by BREFELD. In this plant, according to BREFELD, before pileus formation, the fruit body consists simply of the stem primordium, whose outer hyphae have free ends, and do not enter into the formation of the stem; the pileus primordium is differentiated at the apex "upon the point of the stem," and from this pileus primordium hyphae grow out and turn downward in all directions, forming the "pileus-volva." In the meantime the loose peripheral threads of the stem primordium, the "stem-volva," grow upward to meet these downward growing hyphae from the

apex, and the two groups of threads grow into each other and intermingle to form the common mass of the "volva." In *P. squarrosa* there is a material difference from the condition just described for *C. lagopus*, since in this case there are no hyphae on the stem surface which grow upward and unite with the downward growing threads. Figs. 2, 3, and 7 show the central strand of hyphae just mentioned; in fig. 5 the character of the blematogen hyphae may be seen.

ORGANIZATION OF PILEUS.—Coincident with an early stage in the development of the hymenophore primordium, median longitudinal sections show that the fundament of the pileus is becoming differentiated from the surrounding tissue (fig. 8). The hyphae become richer in protoplasm and by interstitial growth form a more compact structure. This organization proceeds from the center outward in a centrifugal manner, the margin of the pileus keeping pace with, and contributing to, the growth of the hymenophore primordium. During the early stages of differentiation of the pileus some of the hyphae arise from the stem, but its later growth is probably due entirely to interstitial and marginal increase of its own elements, which are interwoven in all directions, thus differing from the hyphae of the stem, which in general run parallel to the stem axis. The pileus elements merge gradually with the blematogen and there is no sharp line of division between the two structures. The cells of the blematogen hyphae, however, are swollen and have thick walls, which stain deeply, while the pileus hyphae are slender and do not take a deep stain after the pileus is well organized, so that a general distinction is evident. In addition, the peripheral threads of the pileus, composing the "cortex," are very compact and form a dark line between the pileus and blematogen, as shown in fig. 13.

FORMATION OF PALISADE LAYER.—Following the stage when the hyphae are arranged in irregular tufts, the hymenophore primordium becomes more compact (fig. 12). The ends of the individual hyphae grow down to nearly the same level and become clavate. This even area is the palisade layer. Serial sections show that it is formed first around the stem, while the hymenophore near the pileus margin is still in the uneven, jagged stage. The

pileus margin at this time is turned downward and often somewhat incurved as a result of epinastic growth, and lies nearly parallel with the surface of the stem, which still slopes outward at a slight angle (fig. 10).

FORMATION OF ANNULAR PRELAMELLAR CAVITY.—During differentiation of the young basidiocarp some ground tissue is left below the hymenophore primordium in the angle formed by the junction of the stem and pileus fundaments. In later development this ground tissue increases to some extent by interstitial growth, but the more rapid growth of the stem, hymenophore, and pileus subjects it to tension, and it very early becomes loose in texture (fig. 4). As the stem elongates and the pileus broadens out, this tension is further increased, so that the ground tissue becomes still looser, with large spaces between the hyphae. At first it only partially tears away from the surface of the hymenophore, and as a result the gill cavity thus formed is weak, with strands of ground tissue traversing it (figs. 13, 14, 16–20). The strength of the prelamellar cavity varies in different individuals, as has been shown to be the case in *Agaricus rodmani* (8); but in any case, in later stages, but long before the gills are exposed by rupture of the veil, the strands of ground tissue become completely broken away, and the edges of the lamellae are entirely free within the gill cavity.

ORGANIZATION OF PARTIAL VEIL.—The terms "blematogen" or "universal veil" and "marginal" or "partial veil" have been interpreted by ATKINSON (5), and are used in the same sense here. The formation of the blematogen has already been described. The radial growth of hyphae in the apex of the young fruit body is very rapid for a time, and a thick layer is formed, enveloping the entire plant, but it is more dense in the apical region (figs 7–9). This rapid growth soon ceases, however, the hyphae become thick-walled and poor in protoplasmic content, the peripheral ones die, and become enlarged and swollen. Because its growth has nearly ceased, the universal veil becomes subject to tension from the expansion of the parts within and breaks up into the large, conspicuous, squarrose scales (fig. 13) which cover the stem and pileus and give the plant its specific name. The partial veil has its origin in

the ground tissue left in the angle between the stem and hymenophore. This tissue increases, both by interstitial growth and by the addition of hyphae which grow down from the pileus margin (fig. 22). By the time that the gills are well formed this tissue occupies a considerable area lying between the margin of the pileus and the surface of the stem, and forming the floor of the gill cavity. It is covered externally by the blematogen, with the inner surface of which its hyphae are interlaced, as some of them are with the stem surface. When expansion of the pileus occurs and the veil is ruptured, it is left upon the stem as an annulate membrane composed of two layers, the coarse, scaly blematogen layer below and the partial veil above.

ORIGIN AND DEVELOPMENT OF LAMELLAE.—In a recent publication ATKINSON (9) has shown that in the Agaricaceae thus far studied there are two types in regard to the origin and development of the lamellae. First, the "*Agaricus*" type, in which the gills arise by downward growing radial salients of the hymenophore, accompanied or preceded by a more or less well developed annular prelamellar cavity. Second, the "*Amanita*" type, in which there is no general annular prelamellar cavity, and the origin of the lamellae is a series of trabeculae extending from the pileus fundament to the stem, and attached to both. *P. squarrosa* obviously belongs to the first type of development, since we have already seen that in the course of development of the young fruit body a general annular, prelamellar cavity, though weak, and a palisade layer are formed.

The origin and differentiation of the gills from the hymenophore is centrifugal; the later formed and younger parts are nearer the margin, becoming progressively older as the stem is approached. Successive stages in the origin and development of the lamellae, therefore, may be studied by means of serial longitudinal sections, commencing at the pileus margin and going toward the center of the fruit body.

Figs. 16–21 represent such a series of sections. The basidiocarp from which they were made was one selected from material imbedded in collodion, and the sections, 15–20 μ thick, were cut with the sliding microtome. The use of collodion (or celloidin) as

an imbedding material obviates the difficulty sometimes met with in the use of paraffin, that delicate structures may be deformed or dislocated by the heat of the oven or in spreading the paraffin ribbons. Furthermore, the cutting of thicker sections, with a sliding stroke, offers little chance for the displacement of structures, which might happen in cutting thin paraffin sections. I mention these points because some might suspect that the tearing away of the ground tissue below the hymenophore, as shown in the following figures, might be due to manipulation of the tissue, but such is not the case.

Fig. 16 represents a section near the margin of the pileus; the hyphae of the hymenophore are growing down in little tufts, and at this time present a very loose, uneven surface. A considerable number of hyphae from the ground tissue below may be seen spanning the prelamellar cavity and united indiscriminately with the downward growing tufts of the hymenophore and with the hyphae in the spaces between them.

In fig. 17, from a section a little nearer the stem, the hymenophore on either side of the section presents the same loose, uneven surface as in the preceding figure; but in the middle the hyphae have enlarged at the tips and become blunt, and the ends have grown down to form an even surface, the palisade, from which the ground tissue is almost entirely broken away. The reason that the palisade is in the middle of the section, with undifferentiated tissue on either side, is readily seen, if we remember that the hymenophore is in the form of a circle around the stem apex, so that tangential sections, in passing toward the center, cut through older parts of the hymenophore in the middle of the section, with younger parts on either side. For further details see the papers on *Agaricus rodmani* and *Coprinus* species by ATKINSON (**8, 9**), where, by means of diagrams, the orientation of the parts of the fruit body in relation to longitudinal sections is made very clear.

In fig. 18, in addition to the undifferentiated tissue on either side and the palisade layer, two slightly downward projecting folds of the latter may be seen. These slight downward projections of the palisade layer represent the first origin of the lamellae in this area. To one a strand of ground tissue is attached, while the other

is completely free. That this ground tissue has nothing to do with the formation of the palisade is shown by the fact that, as already stated, it is attached indifferently to the hymenophore primordium, and in many cases is largely broken away from the tufts and between them before the palisade layer is formed. Furthermore, these tufts of the hymenophore primordium are not the primordia of the lamellae, since before the origin of the latter they become lost in the even palisade (figs. 17, 18). In those instances where the ground tissue remains adherent to the edges of the lamellae for some time, and not to the palisade between them, it is due to the fact that through the downward growth of the gills the strands of hyphae attached to their edges are subject to less strain than the hyphae attached between them, and so keep their attachment longer.

The downward growth of the lamellae may be partly initiated by the pressure in the palisade layer due to the rapid growth and enlargement of its hyphae, which would produce a tendency to throw the palisade into folds. The chief agency in their formation, however, seems to be the downward growth of radially arranged groups of hyphae in the hymenophore, which are very active in growth at this time, as indicated by their deep stain. These radial lines of deeply staining hyphae push down into the folds of the palisade and form the trama of the gills (figs. 19–21). The further growth of the lamellae in depth takes place by apical and interstitial growth in the trama. Later stages in development (fig. 23) show the hyphae from the trama turning outward on all sides to add to the growth of the palisade layer of the gills.

Pholiota flammans

PRIMORDIUM OF BASIDIOCARP.—The very young fruit body, before any internal differentiation has taken place, is a compact structure, composed of slender, intricately interwoven hyphae, 2–3 μ in diameter, and rich in protoplasm. The hyphae have a general direction of growth away from the substratum, and many free hyphal ends radiate outward all over the surface of the basidiocarp, so that the peripheral area is somewhat looser in structure than the compact central region (fig. 24). This loose radiating zone of hyphae upon the outside represents an early stage in the

development of the blematogen, which is probably present from the first appearance of the fruit body primordium.

DIFFERENTIATION OF STEM FUNDAMENT.—As development proceeds, the hyphae in the base of the primordium take on more active growth than the others, and by interstitial increase form a very dense structure. This new area of growth, which is the stem fundament, is shown as a deeply stained region in the base of the fruit body in fig. 25. As growth continues, the cone-shaped stem fundament advances toward the apex of the fruit body. In fig. 26 the most deeply stained portion represents the rapidly growing, progressive apex of the stem fundament; the more compact tissue below represents its earlier differentiated base; and the outer zone of loose tissue surrounding the whole is the blematogen.

DIFFERENTIATION OF HYMENOPHORE AND PILEUS PRIMORDIA.—The first evidence of the hymenophore primordium is the appearance of a ring of compact, slender hyphae which surrounds the upper part of the stem fundament and grows down into the ground tissue, clothing the latter. The appearance of these differentiated hyphae marks off the pileus area from the stem fundament. In some cases the pileus fundament probably exists before the appearance of the hymenophore primordium, as indicated by the slight divergence of the hyphae from the apex of the stem fundament or by the more rapid growth in the region of the future pileus; but no sharp distinction can be drawn between the fundaments of pileus and stipe until the primordium of the hymenophore is differentiated. An early stage in the development of the latter is shown in fig. 30. As development continues, the pileus and hymenophore progress together in growth in a centrifugal manner. New elements from the pileus margin contribute to the hymenophore primordium, which also increases by interstitial growth. Interstitial growth also takes place in the pileus primordium, making it more compact. In the stage of figs. 31 and 32 the stem and pileus are well organized and the hymenophore has become compact, with uneven surface. The palisade is formed later, as shown in figs. 34 and 37. The hyphae are not as crowded, or so conspicuously clavate, as in *P. squarrosa*.

BLEMATOGEN.—The blematogen is present from the first appearance of the fruit body primordium. During early development

it radiates from all parts of the surface as a loose aggregation of hyphae with numerous interhyphal spaces (fig. 29). The new elements arise chiefly in the apex of the young fruit body and extend outward in a radial direction, curving backward as the fundament of the basidiocarp elongates and as the stem and pileus primordia are differentiated. This peculiarity of the blematogen is like that in *P. squarrosa.* This downward growth continues until a thick covering is formed (fig. 31). The elements of the blematogen are thick-walled and somewhat larger than the other hyphae of the basidiocarp, but they are not conspicuously globose, as in *P. squarrosa.*

Early in its formation some of the threads begin to break down and gelatinize, and the universal veil soon becomes a gelatinous matrix, imbedded in which may be recognized the remnants of hyphae not yet disorganized. Such a condition exists in fig. 31, and a high magnification (fig. 38) shows a sharp contrast between the gelatinized blematogen and the cortex of the pileus at this stage. A very similar condition of the universal veil has been noted in *Stropharia ambigua* by ZELLER (**25**).

The disorganization of the blematogen elements does not go beyond the degree shown in fig. 38. Sections perpendicular to the pileus in mature specimens show a very similar condition; there is a gelatinous ground substance filled with dead hyphae whose general course is parallel to the surface of the pileus. Through drying of the outer part and the tension exerted upon it by the expanding pileus the blematogen breaks up into scales. These scales differ very markedly, however, from the stout, pointed scales of *P. squarrosa;* they are thin and delicate and more or less fibrillose in nature.

The gelatinization takes place only over the pileus, the blematogen clothing the stem very nearly resembling that of *P. squarrosa.* For this reason the scales covering the pileus in the mature plant are more delicate than those covering the stem, as indicated in the description of *P. flammans* in SACCARDO'S *Sylloge* (**23**), in which it is stated that the pileus is covered with superficial scales, while the stem is scaly-squarrose.

FORMATION OF ANNULAR GILL CAVITY AND MARGINAL VEIL.—The formation of the gill cavity agrees in all essentials with its

formation in the preceding species. The ground tissue is loose from a very early stage, and through expansion of the different parts of the fruit body it becomes torn away from the lower surface of the hymenophore. This separation from the hymenophore is completed at an earlier stage than in *P. squarrosa*, and consequently a well defined cavity is present before the origin of the lamellae (figs. 34, 37).

During the development of the hymenophore primordium and the breaking away of the ground tissue below hyphae are growing down from the pileus margin. These threads penetrate the ground tissue below the prelamellar cavity and mingle with those on the surface of the stem. In fig. 33 they may be seen curving inward from the pileus margin. In the stage represented here they have not yet reached the surface of the stem, and the loose ground tissue surrounding the latter may still be seen between it and the advancing hyphae from the pileus margin. These threads are sharply contrasted with the other tissue of the basidiocarp because of their short cells, which in some cases are as broad as they are long. In addition, they may be distinguished from the blematogen external to them by their deeper stain. These hyphae from the pileus margin, together with the ground tissue below the hymenophore, form the partial veil; it tears away from the stem at an early stage in the expansion of the plant, and may in some cases hang down from the pileus margin as a thin appendiculate veil.

ORIGIN AND DEVELOPMENT OF LAMELLAE.—The origin and development of the gills in this plant does not differ materially from the condition already described for *P. squarrosa*. Here we have a better defined gill cavity, with no ground tissue traversing it and connecting with the palisade layer. The latter is composed of hyphae with blunt ends, standing in an even surface, compact, but not crowded. Serial longitudinal sections, from the tangential to the median, show that the formation of the annular gill cavity, of the hymenophore, and the development of the lamellae, all proceed by centrifugal growth; that is, the older and first formed parts of these structures lie near the stem and progress by differentiation and growth toward the periphery of the fruit body. As has already

been stated, the hyphae in the palisade layer are not crowded enough to produce any great pressure, and it would seem that the origin of the gill salients, which appear as downward folds of the palisade, is due entirely to the growth and elongation of radial lines of hyphae in the hymenophore, which push the palisade down in folds, the young gills, as described for *Hypholoma sublateritium* (1) and *Stropharia ambigua* (25). The gill salients are broader than in *P. squarrosa*, and this may be due to the fact that when thrown into folds by downward growth of the hyphae above, because of the less crowded condition of the palisade, they are not subjected to as great lateral pressure as in that species.

Fig. 39 is from a tangential longitudinal section of a basidiocarp with sterile gills, that is, the palisade layer has failed to form. The cystidia, which develop from the trama of the gill, are very noticeable as deeply staining clavate bodies. The situation presented here is interesting because of its bearing on the question recently raised by LEVINE (21) in regard to the origin of the lamellae in the Agaricaceae. The points of growth for the origin of the lamellae, as described by ATKINSON in several species of the Agaricaceae, including *Agaricus rodmani* (8) and *Coprinus comatus*, *C. atramentarius*, and *C. micaceus* (9), occur in radial areas of hyphae in the hymenophore, which develop centrifugally and grow down more rapidly than the other hyphae. These areas are the gill tramae, and push the palisade into regularly spaced folds, which are the salients of the lamellae themselves. This method of origin of the lamellae occurs in the three species described here.

According to LEVINE'S conception, radiating ridges of palisade cells arise in the fundamental tissue, and by continued differentiation and downward growth of new palisade cells, split apart. The adjacent halves of neighboring ridges then come together and unite to form a lamella. The trama of the gill would thus be formed by the coming together of preexisting palisade cells from adjacent ridges. If no palisade cells were differentiated, therefore, no trama could be formed. In this case, however, no palisade cells are formed, yet the trama of the gill and the cystidia, which come from trama tissue, develop normally.

Pholiota adiposa

PRIMORDIUM OF BASIDIOCARP.—In the youngest fruit body sectioned the mycelial threads grow out from the substratum to form a compact mass of hyphae which are closely interwoven and run in all directions. From this structure hyphae gradually assume an upward direction of growth, forming a papilla-like projection (fig. 42), the fruit body primordium. The threads in the basal mycelium from which the fruit body arises are very uneven in size; those of the primordium are even in size, with free ends radiating out all over the surface.

STEM FUNDAMENT.—The stem fundament probably differentiates first in the base of the fruit body, as in the preceding species. In fig. 43 its apex appears as a compact, dark-staining region near the top of the basidiocarp, surrounded by the looser tissue of the young blematogen. The fundament hyphae are very slender at first, dense in protoplasm, and closely intermingled, running in all directions.

PRIMORDIA OF HYMENOPHORE AND PILEUS.—When the hymenophore and pileus primordia appear, the stem has become well organized as a compact conical area, surrounded by the loose universal veil. The first differentiation of the pileus fundament becomes evident through the growth of hyphae upward from the stem apex; these spread outward laterally, so that at this stage the stem and pileus areas together resemble a sheaf of wheat. At the same time some of these hyphae become subject to strong epinastic growth, and curve down in a ring around the stem apex, forming the primordium of the hymenophore, which definitely differentiates the pileus area from the stem fundament. The growth of the pileus continues by interstitial and marginal increase of its elements, and the hymenophore broadens out by growth within itself and by intercalary growth from the pileus margin, with which it keeps pace. The hyphae of the hymenophore primordium often become aggregated into tufts (fig. 48), as in *P. squarrosa*. Ground tissue may still remain attached to these tufts. The hyphae now grow down to the same general level, their ends become blunt, and form an even surface. During early development the hymenophore extends down on the stem farther than in the two preceding

species (figs. 45, 47). In later stages it loses this decurrent character.

BLEMATOGEN.—The universal veil exists from the beginning; its development proceeds very much as in *P. flammans*. At first its hyphae radiate from all over the surface of the basidiocarp. Later the growth of new elements is largely confined to the apex. The peripheral cells become enlarged, thick-walled, with a diminution in protoplasmic content (fig. 52). The outer ones appear empty and dead. Gelatinization takes place here, as in *P. flammans*, but later, after the gills are well formed. Sections through the mature pileus show that the blematogen has a structure very comparable in the two species, in either case composed of a structureless matrix in which are imbedded dead hyphae, with a general course parallel to the pileus surface. At first disorganization occurs only over the pileus, but in the mature plant the gelatinization takes place over the entire surface.

The mature pileus in *P. flammans* is dry, and in *P. adiposa* is gelatinous or viscid. This difference is due to the fact that in the latter species the disorganization of the blematogen elements proceeds farther than in the former, so that the walls of the hyphae become more gelatinous, with a greater capacity for absorbing water. The surface of the blematogen breaks up into scales, as in *P. flammans*, but the scales are very different in character. They are not thin and fibrillose here, but in wet weather appear like little lumps of jelly on the surface and are easily lost, so that it is not uncommon to find old fruit bodies with the surface of the pileus nearly free from them, especially over the central area.

ANNULAR PRELAMELLAR CAVITY.—The gill cavity begins to develop soon after the appearance of the hymenophore and pileus primordia. The growth and expansion of these parts tear apart the ground tissue below the former, making it loose, with large spaces between the hyphae. At first, strands of hyphae span the cavity and remain attached to the hymenophore, but these have all disappeared by the time the palisade layer is formed, and the cavity is then clear (fig. 47).

MARGINAL VEIL.—The partial veil is composed of the ground tissue left in the angle between the hymenophore and stem, together

with some hyphae which grow down from the pileus margin. This growth, however, is not as strong as in *P. flammans*. The partial veil is covered externally by the blematogen. It ruptures at the pileus margin during expansion of the plant, leaving a thin and fugacious annulus on the stem.

ORIGIN AND DEVELOPMENT OF LAMELLAE.—The origin and growth of the gills take place in this species much as in *P. flammans*. The first evidence of the origin of the gill salients is the downward projection of the palisade layer in broad folds (figs. 50, 51). A single one of these broad folds includes several of the tufts which earlier appear in the hymenophore primordium and become lost in the palisade; consequently, these tufts cannot be considered as gill fundaments or directly concerned in their origin. At the apex of the folds the ends of the palisade cells may in some cases spread slightly apart, showing that considerable pressure is exerted by the downward growing hyphae from the hymenophore above. Under no circumstances, however, do the gill salients show any evidence of splitting; the hyphae merely spread slightly apart at the ends, and in later stages come together again to form an uninterrupted palisade. Serial sections show that the formation of the gill salients is radial and centrifugal.

Figs. 53, 54, and 55 show a condition that might easily lead to a wrong interpretation of the origin of the lamellae by one not familiar with the orientation of the parts involved. A similar condition existing in *Agaricus rodmani* has been explained by ATKINSON (8) and so will not be gone into in detail here. The sections are tangential in the margin of the pileus at a stage in development when the pileus margin is enrolled. The attachment of the gill trama both above and below does not mean that the trama of the gill has grown down and united with the tissue below, as might appear at first glance. The pileus margin, and consequently the hymenophore, is incurved so that the hymenophore lies both above and below the gill cavity, and the attachment of the trama below as well as above represents its point of origin. The direction of growth of the trama is not in the plane of the section, but perpendicular to it. A similar condition exists in *P. squarrosa* and *P. flammans* at a certain stage in the organization of the pileus before it has expanded.

Sequence of plant parts

The relative time of origin of the primordia of the basidiocarp is of some historical interest. FRIES (17), influenced perhaps by the preformation theory, still in vogue in his time, believed that all the parts, pileus, stem, and hymenophore, although indistinguishable, existed already formed in the young fruit body and unfolded simultaneously. SCHMITZ (24) held that a successive formation of new parts occurred; that the development of new parts rose upward just as gradually as in the higher plants, so that those standing higher came into evidence later than those below; and that therefore the matrix developed before the stipe, the latter before the pileus, and the latter before the hymenium. Later, FAYOD (15) formulated a general law to the effect that the first part to be differentiated is always the pileus primordium.

More recent work has shown that no general rule can be laid down as to what primordium shall have precedence in differentiation. In *Agaricus campestris* (2), *A. arvensis* (3), *A. rodmani* (8), *Armillaria mellea* (4), and *Stropharia ambigua* (25), the hymenophore primordium is differentiated first. In *Hypholoma sublateritium* (1), *H. fasciculare* (11), and *Amanitopsis vaginata* (7) the pileus area is first outlined. The formation of the stem fundament is the first differentiation to take place in *Lepiota cristata* and *L. seminuda* (10), several species of *Cortinarius* (14), *Rozites gongylophora* (22), and the 3 species of *Pholiota* described.

Even in the same species variations may occur as to the relative time of appearance of the different primordia. ATKINSON (10) has shown this to be probable in *Agaricus arvensis* (3) and *Lepiota clypeolaria* (6). In *P. flammans* it would appear that the fundament of the pileus in some cases differentiates before the hymenophore primordium, and this may be true of the other two species described. In all 3 species, however, the appearance of the stem fundament precedes the other primordia of pileus and hymenophore.

Summary

1. The basidiocarp primordium consists of slender hyphae intricately interwoven; they are arranged more loosely in the

peripheral region, and radiate from the entire surface of the fruit body.

2. The blematogen is present from the first differentiation of the fruit body primordium, and in its earliest stages consists of the loose, radiating peripheral hyphae. In subsequent growth it forms a thick layer enveloping the entire plant; in *P. flammans* and *P. adiposa* it becomes partially disorganized by gelatinization.

3. The formation of the stem fundament is the first differentiation to take place in the young fruit body. It originates in the basal part of the basidiocarp and by growth and differentiation progresses toward the apex.

4. The primordium of the hymenophore is differentiated around the apex of the stem fundament as an annular internal zone of new growth. Frequently, before the hymenophore appears, a slight divergence of hyphae from the stem apex indicates differentiation of the pileus. When the hymenophore primordium is differentiated, it marks off clearly the limit between the pileus and stem. It consists of slender hyphae, rich in protoplasm, which grow downward. At first the lower surface is uneven and loose, but by continued growth the hymenophore becomes compact and the hyphae grow down to the same level, forming an even palisade area. The growth of the hymenophore and organization of the pileus proceed centrifugally.

5. The annular prelamellar cavity is formed by the tearing away of the ground tissue from the lower surface of the hymenophore, due to the tension exerted by the growth and expansion of the plant parts. It is weak in *P. squarrosa*, and well formed in *P. flammans* and *P. adiposa*, before the origin of the lamellae.

6. The marginal veil consists of two layers; the inner portion is composed of the ground tissue left in the angle between the stem and the hymenophore after their differentiation, which increases by its own growth and by the addition to it of hyphae from the pileus margin. The outer portion is a section of the universal veil between the pileus margin and the surface of the stem.

7. The lamellae originate as a series of radiating areas of active hyphae in the hymenophore, which grow down and push the palisade layer into folds. The points of growth for the origin of the gills are

in these downward growing areas in the hymenophore, and the first folds in the palisade are the salients of the lamellae themselves. In *P. flammans* and *P. adiposa* the gill salients are very broad; in all 3 species their origin and differentiation is centrifugal and their subsequent growth is downward into the gill cavity.

In conclusion, I wish to acknowledge my deep obligation to Professor G. F. ATKINSON, under whose direction this work was done, for his unfailing interest and many helpful suggestions.

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EXPLANATION OF PLATES XVI–XX

The following microphotographs were made with the Bausch and Lomb vertical camera and Zeiss lenses, and with a horizontal Zeiss camera.

PLATES XVI, XVII

Pholiota squarrosa

Fig. 1.—Median section, showing apex of stem fundament as dark-stained area near center of figure; very deeply stained hyphae scattered through stem fundament; hyphae of blematogen radiating from summit; ×50.

Fig. 2.—Slightly older stage than above, showing central strand of hyphae that curve downward from summit to form blematogen; ×50.

Fig. 3.—Median section, showing radiation of blematogen hyphae and their loose arrangement at periphery of fruit body; ×50.

Fig. 4.—Median section at a stage closely following differentiation of hymenophore; cone-shaped stem fundament occupies lower part of figure, with hymenophore primordium on either side of deeper stained apex, showing as two small, deeply stained areas, which differentiate pileus primordium above from stem fundament; below hymenophore primordium ground tissue is becoming loose in structure; outside the whole is the thick universal veil; ×33.

Fig. 5.—Left side of same section, magnified more to show character of blematogen; at extreme left are enlarged, thick-walled, empty cells of outer

portion of blematogen; at extreme right may be seen a part of hymenophore primordium with loose ground tissue below; ×56.

FIG. 6.—Left side of median section about the time when hymenophore primordium is first differentiated; tangled, compact mass of hyphae of very young hymenophore near center, with looser ground tissue surrounding it; ×133.

FIG. 7.—Median section at about the same stage of differentiation as fig. 4; two compact, dark spots are hymenophore primordium; from summit blematogen hyphae are curving outward and downward; ×50.

FIG. 8.—Median section; conical stem fundament below; hymenophore primordium on either side, and pileus fundament appearing above hymenophore as a more compact, central area; loose ground tissue clothes stem, and outside is deep-stained blematogen; ×18.

FIG. 9.—Tangential section of same fruit body; hymenophore primordium appears as dark horizontal area, with uneven lower surface; irregular dark region just below is oblique section of stem surface; ×18.

FIG. 10.—Median section, at a stage when palisade has formed; gill cavity appears as a narrow slit almost closed because of epinastic growth of pileus margin; below, the looser ground tissue; ×133.

FIG. 11.—Tangential section of same fruit body; ground tissue is tearing away from hymenophore to form gill cavity; above hymenophore is crescent-shaped pileus, with the much thicker blematogen outside; ×33.

FIG. 12.—Higher magnification of section near preceding to show blunt ends of palisade hyphae, with loose ground tissue below; above is dense hymenophore; ×133.

FIG. 13.—Blematogen has broken into scales; stem and pileus are well organized; below hymenophore on either side is gill cavity, weak, with strands of ground tissue traversing it; dark line between pileus and hymenophore indicates area of more rapid growth; ×13.

FIG. 14.—Left side of a section similar to fig. 13, and showing same features enlarged; ×32.

FIG. 15.—Tangential section, showing compact hymenophore; no gill cavity in this section because its centrifugal development has not yet reached tangential area here shown; ×18.

FIGS. 16–20.—Serial tangential sections from pileus margin toward stem; in fig. 16 hymenophore is uneven and gill cavity is weak, with considerable ground tissue still attached to hymenophore; in fig. 17 hymenophore has become even in center, forming a palisade area; gill cavity is stronger than in preceding section; in fig. 18 two gill salients appear as folds in level palisade; figs. 19 and 20 show older stages of these and other salients nearer stem; ×32.

FIG. 21.—Higher magnification of fig. 20, showing origin of gill tramae in hymenophore as regularly spaced, deeper staining areas of rapidly growing hyphae; ×128.

FIG. 22.—Left side of median section in a stage after lamellae are well differentiated; at extreme left are hyphae growing down from the pileus margin into ground tissue below; knife has passed lengthwise through a gill, making it thin enough to look through and see level palisade between it and next gill; ×128.

FIG. 23.—Tangential section, showing gills with trama and palisade; ×148.

PLATES XVIII, XIX

Pholiota flammans

FIG. 24.—Median section of very young fruit body, which is broken just above substratum of rotten wood; loose, radiating threads represent early stage in formation of blematogen; no internal differentiation has taken place; ×60.

FIG. 25.—Stem fundament forming in base of fruit body, its apex stained very deeply; outside is blematogen; ×36.

FIG. 26.—Slightly later stage in which, by progressive growth, apex of stem fundament has advanced to summit of fruit body; ×36.

FIG. 27.—Somewhat older fruit body, with stem fundament differentiated, apex showing near summit as darker area; very deeply stained, isolated hyphae are scattered through stem fundament; ×36.

FIG. 28.—Same as fig. 27; ×36.

FIG. 29.—Older fruit body, with blematogen radiating from entire surface; stem area well organized, but no other differentiation; ×36.

FIG. 30.—Small area on either side with looser ground tissue below represents very young hymenophore; below is conical stem area and above is pileus fundament which is partially organized; over pileus area blematogen hyphae are spreading downward and have begun to gelatinize; on sides blematogen hyphae are still radiating laterally; ×20.

FIG. 31.—Stem and pileus areas well organized; hymenophore shows as very deeply stained area on either side below pileus; hyphae from pileus margin are shown growing down and uniting with stem surface; outside is lighter stained, partially gelatinized blematogen; ×36.

FIG. 32.—Tangential section of same, showing uneven stage of hymenophore, with ground tissue in gill cavity; ×36

FIG. 33.—Left side of median section; uneven surface of hymenophore primordium is shown above weak gill cavity; outside hymenophore, hyphae from pileus margin are growing in toward stem surface; majority of these hyphae have not reached stem and ground tissue is seen between them and the latter; at extreme left is blematogen; ×86.

FIG. 34.—Right side of median section at a later stage; gill cavity well formed; above it hymenophore has organized palisade near stem, but is still uneven near pileus margin; short-celled hyphae from latter are filling in ground tissue below cavity to help form partial veil; ×142.

FIG. 35.—Tangential section, showing early stage in organization of palisade by hymenophore; gill cavity below; ×125.

FIG. 36.—Tangential section very near stem, showing two broad gill salients, covered by palisade; some clavate cells of latter project beyond surface, giving rough appearance; note disorganized condition of universal veil; ×86.

FIG. 37.—Tangential section, showing even palisade and large gill cavity; ×31.

FIG. 38.—Section highly magnified to show contrast between pileus and gelatinized blematogen; ×142.

FIG. 39.—Tangential section of fruit body with sterile gills; note absence of any palisade, and the cystidia, which develop from trama tissue of gill; ×142.

FIG. 40.—Tangential section, showing normal gills at about same stage as preceding; hyphae of trama may be seen turning outward to contribute to palisade; cystidia are visible on edges of lamellae; ×142.

FIG. 41.—Tracheid of *Picea* inclosed in tissue of stipe; this fruit body was in advanced stage of development, with lamellae well differentiated; ×230.

PLATE XX

Pholiota adiposa

FIG. 42.—Median section of very young fruit body; narrow, dark area in center is a bit of substratum inclosed in tissue; threads radiating from surface form young blematogen; ×50.

FIG. 43.—Later stage, showing apex of stem fundament at summit of basidiocarp; ×56.

FIG. 44.—Still later stage in development; ground tissue is becoming loose around apex of stem fundament; blematogen hyphae have largely ceased lateral growth and are radiating out from summit of fruit body; ×33.

FIG. 45.—Median section of stage when stem and pileus are well organized and hymenophore is forming palisade; heavy blematogen shows no signs of disorganization that occurs later; ×18.

FIG. 46.—Tangential section at same stage in development; because it is nearer pileus margin hymenophore has not formed palisade in this section; ×18.

FIG. 47.—Left side of median section; note that hymenophore is decurrent on stem at this stage; gill cavity is clearly differentiated and free from ground tissue; ×154.

FIG. 48.—Tangential section near pileus margin; uneven hyphae of hymenophore primordium are aggregated into tufts; gill cavity is just beginning to form by tearing away of ground tissue from hymenophore; ×154.

FIG. 49.—Section of same fruit body, but nearer stem; palisade forming in middle region of hymenophore surface; ×93.

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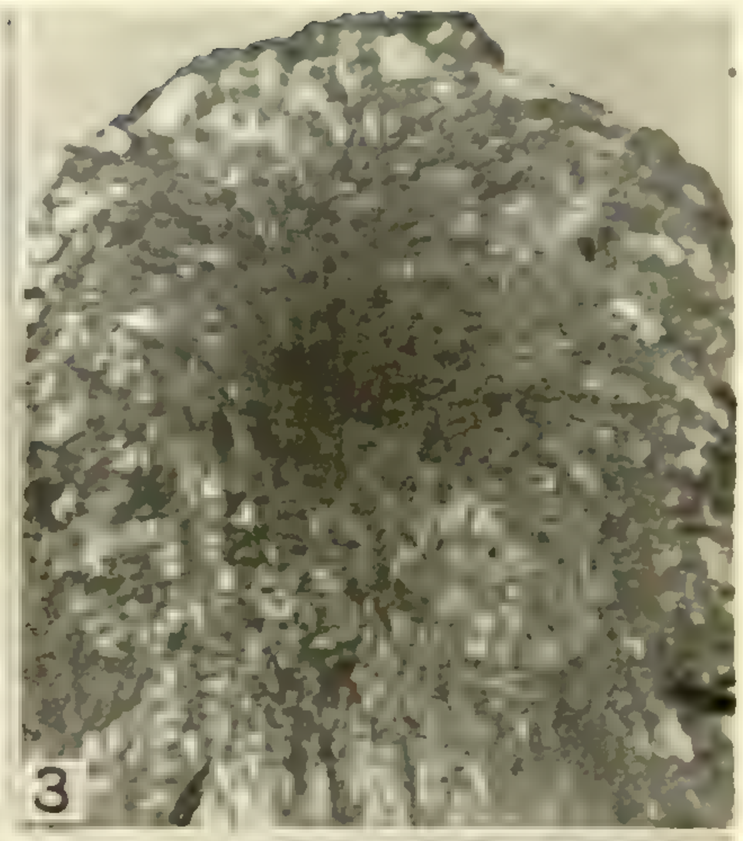
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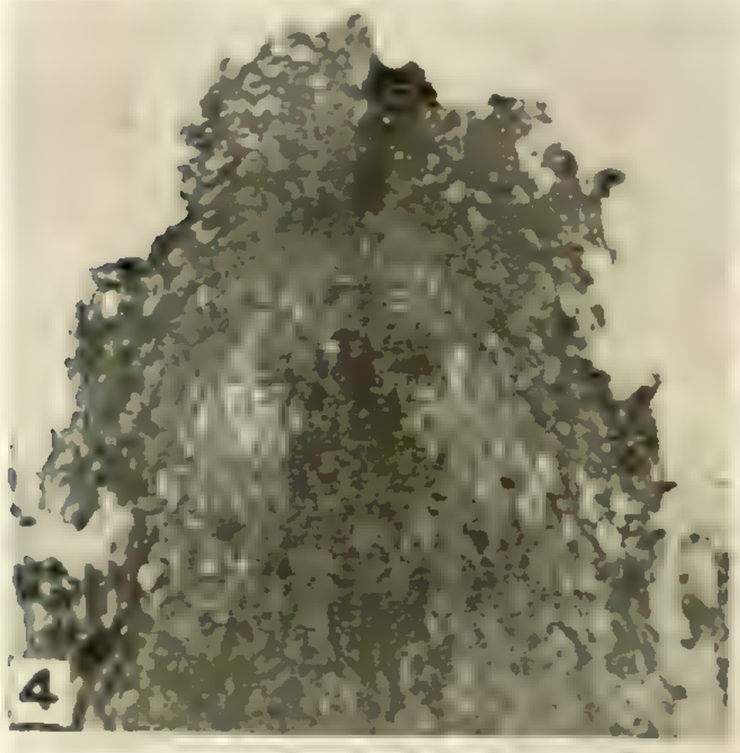
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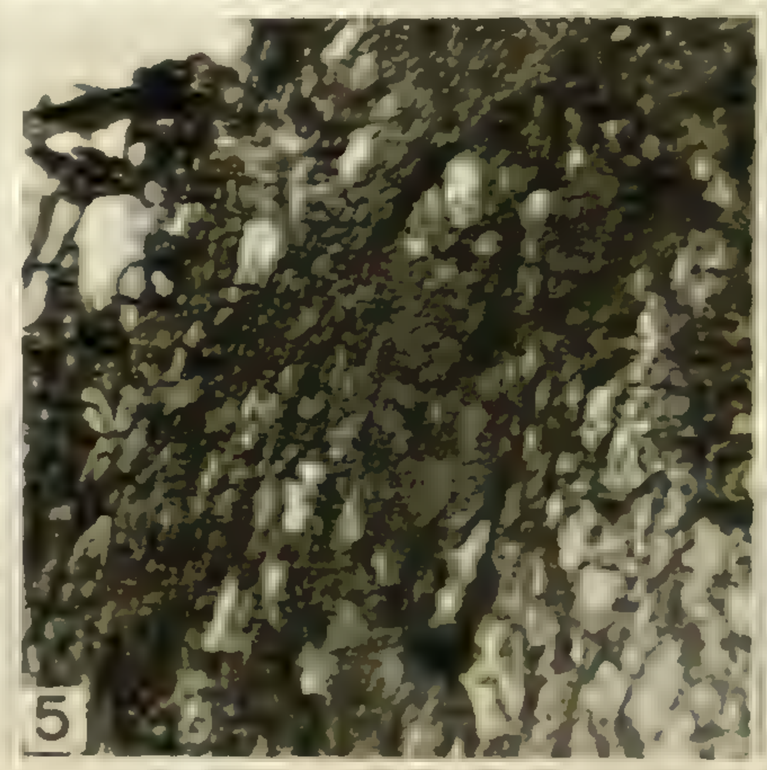
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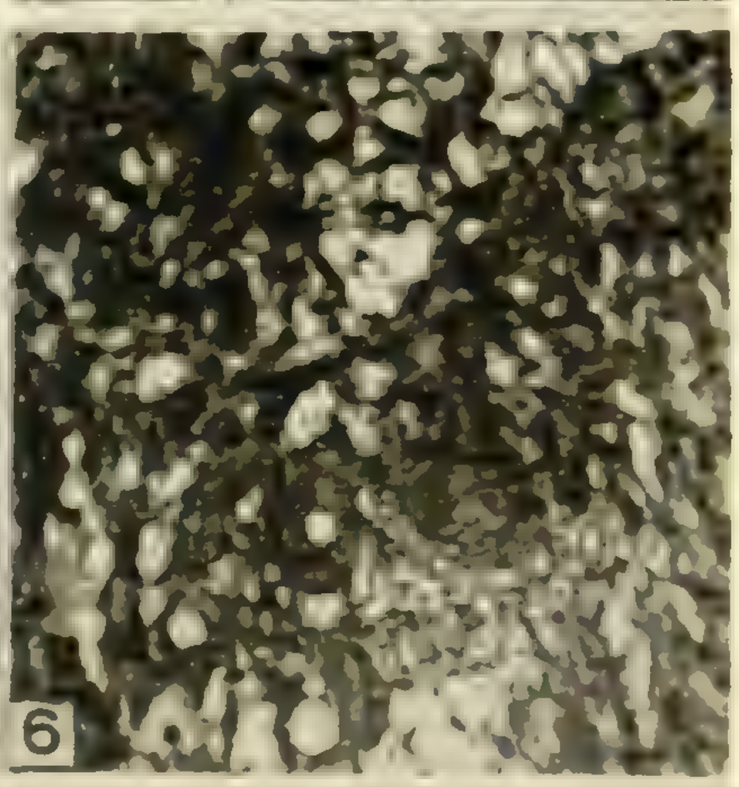
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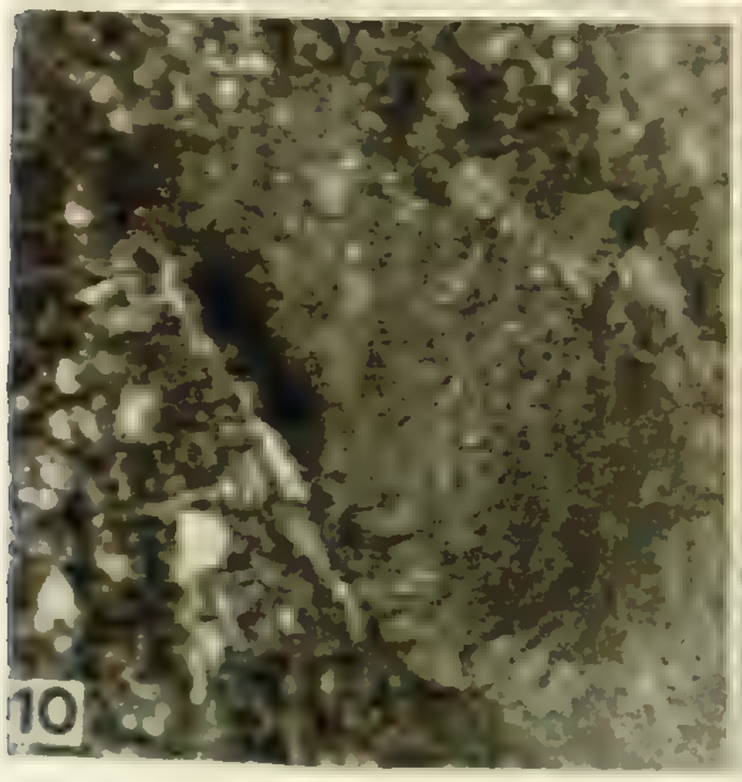
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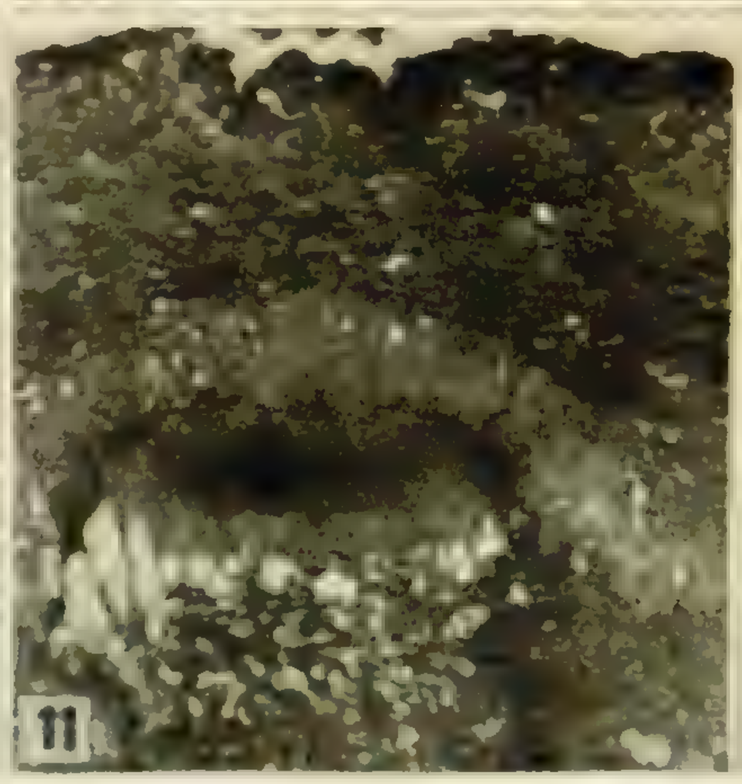
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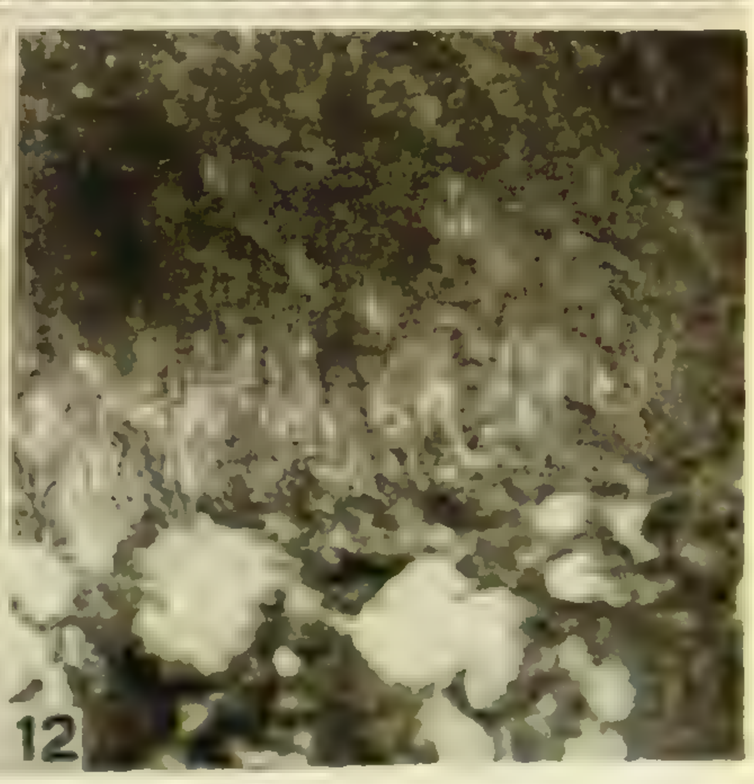
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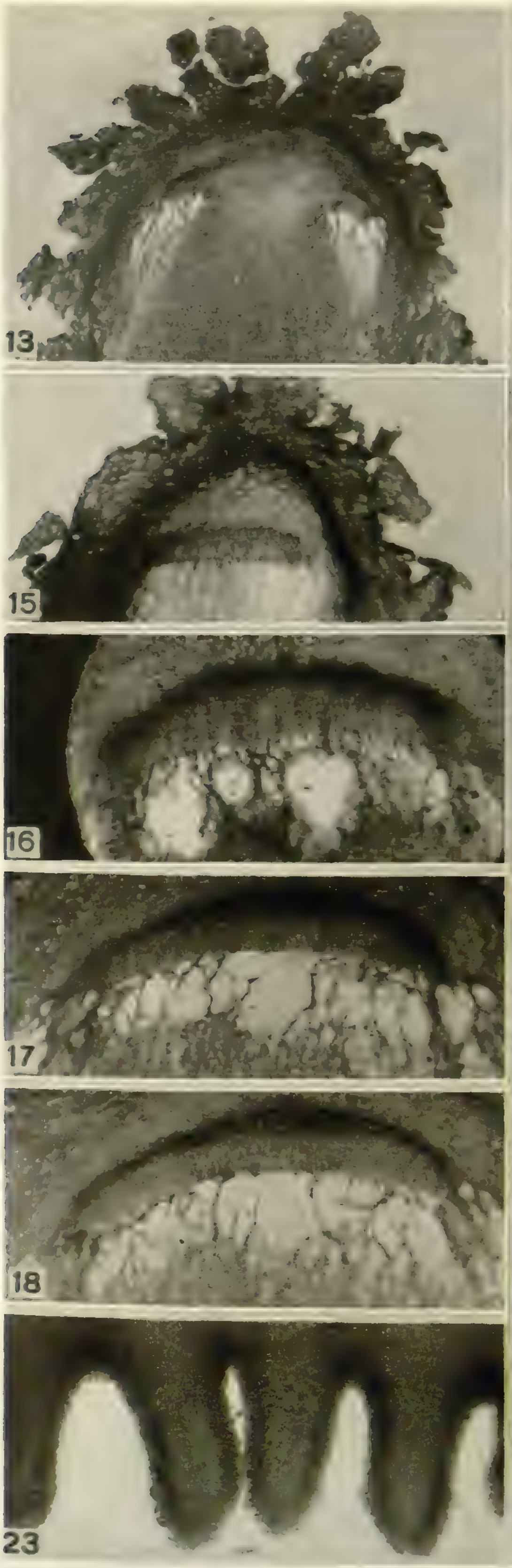

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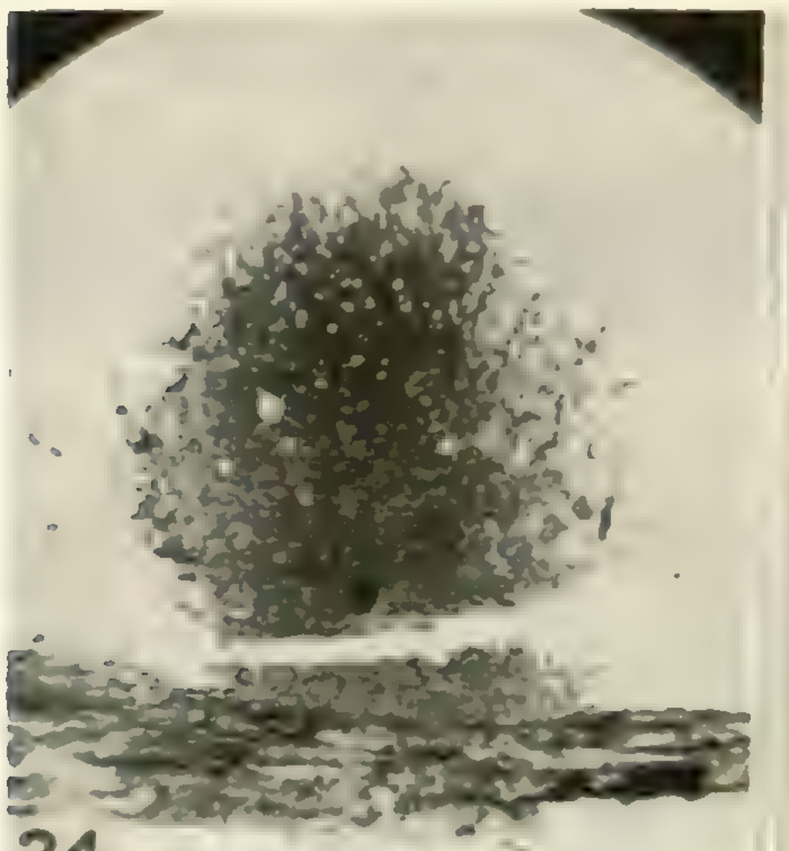
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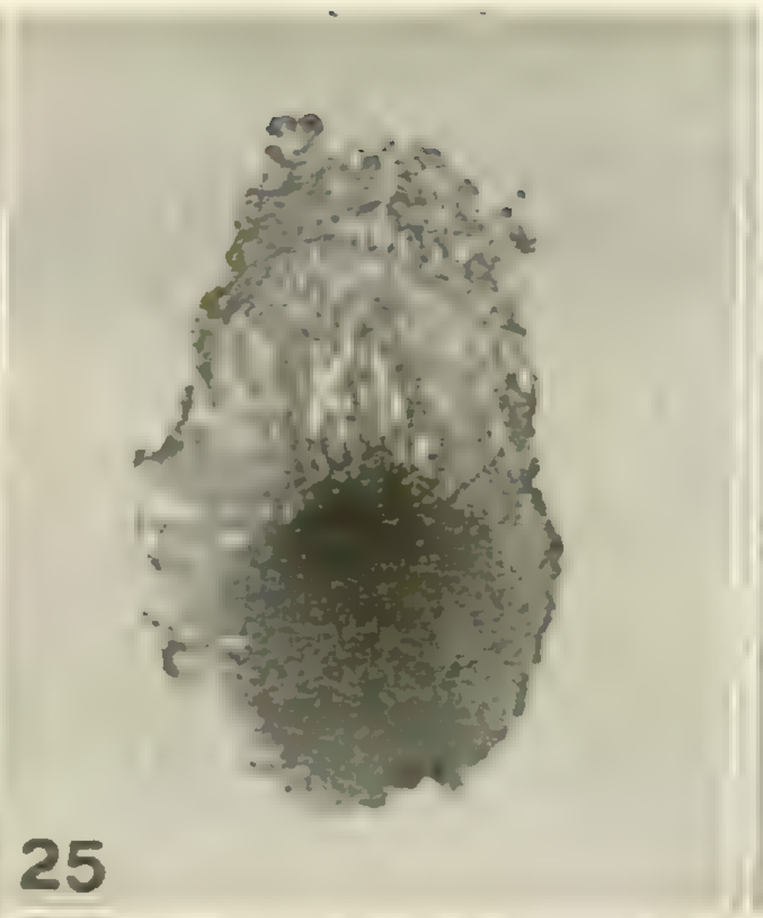
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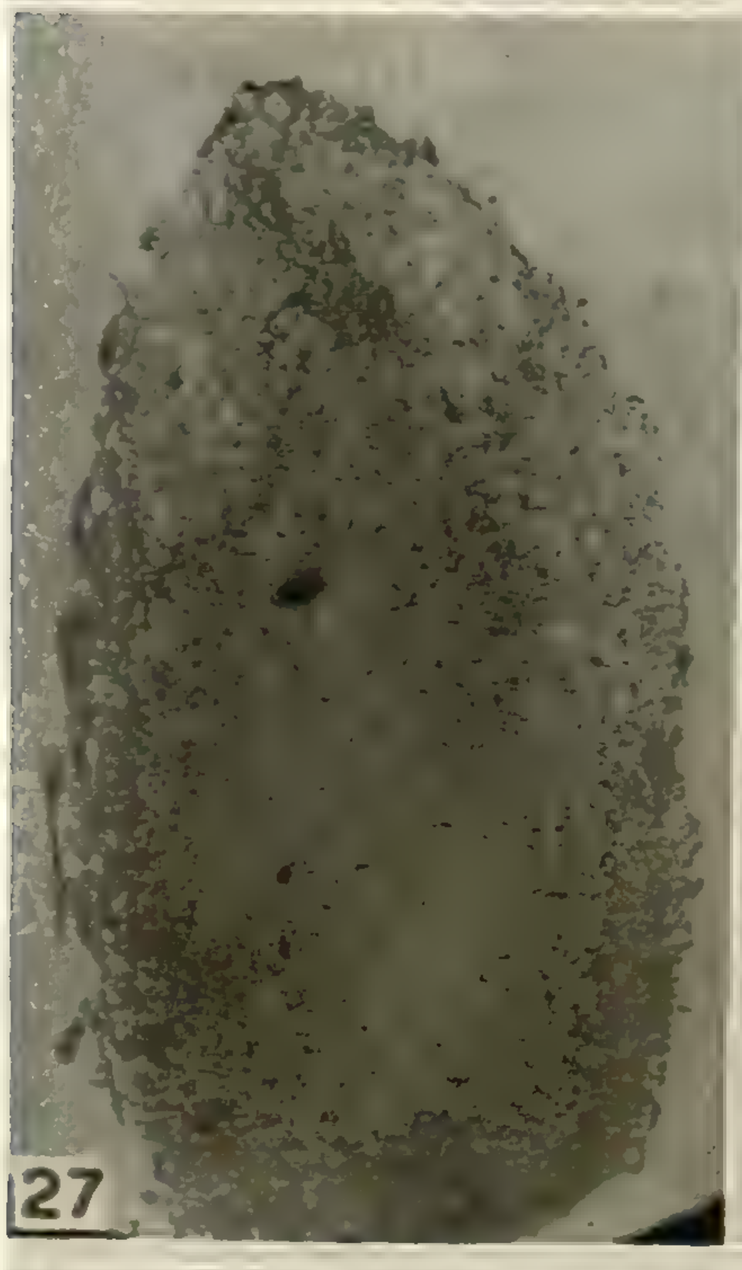
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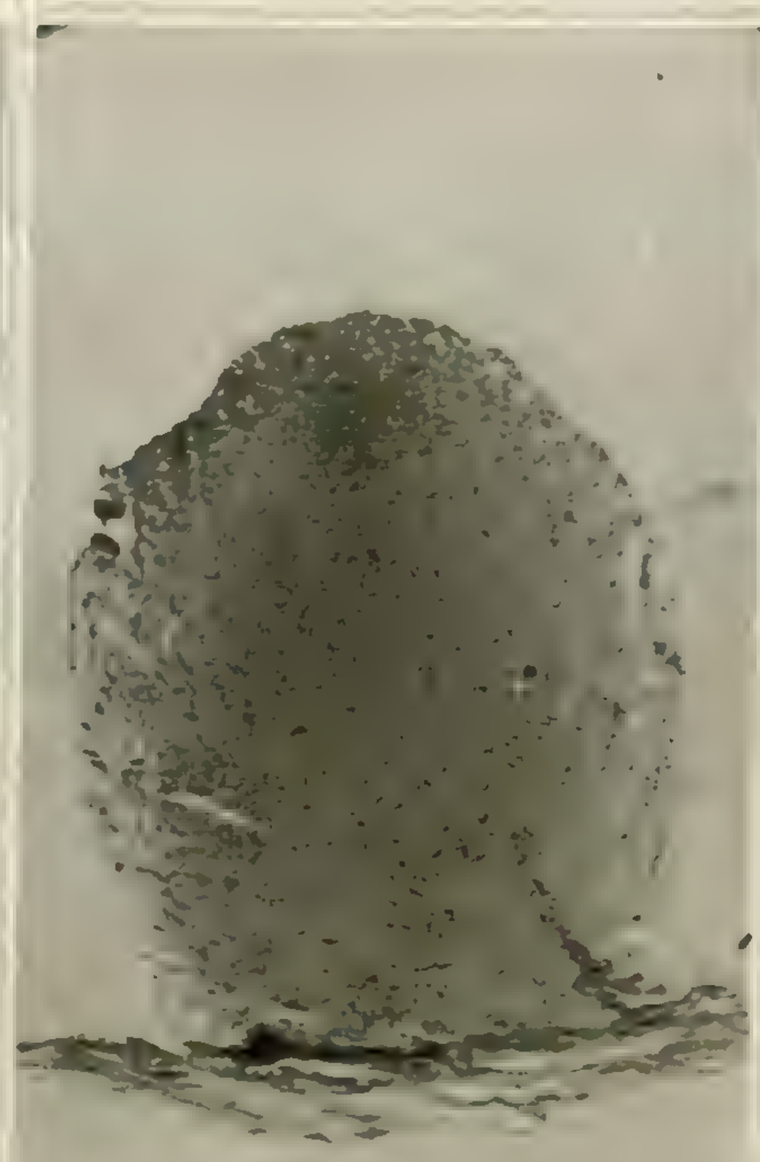
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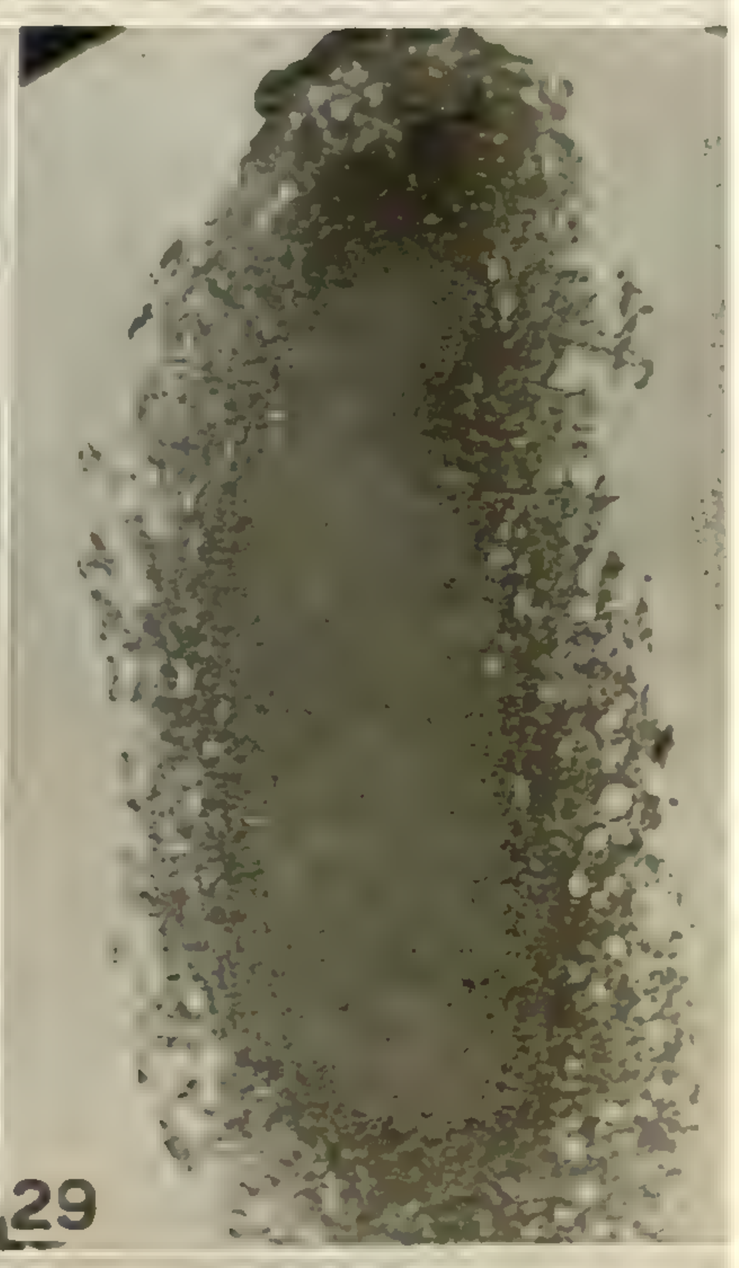
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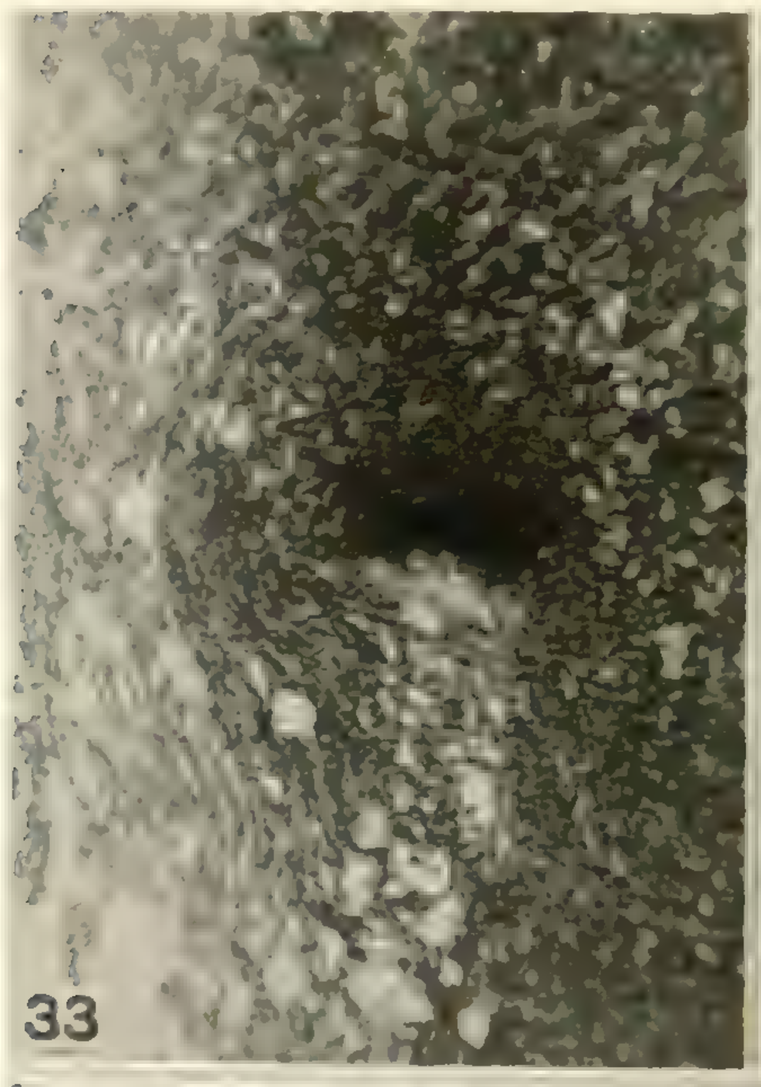

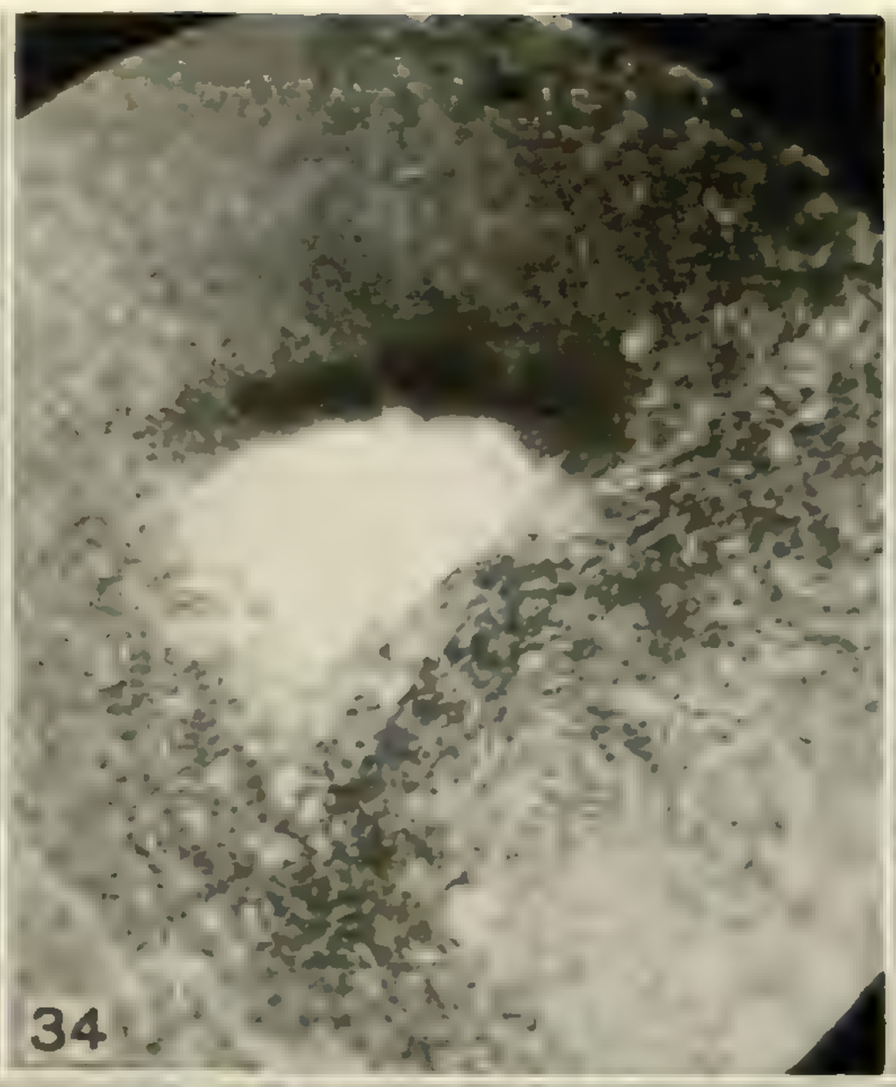

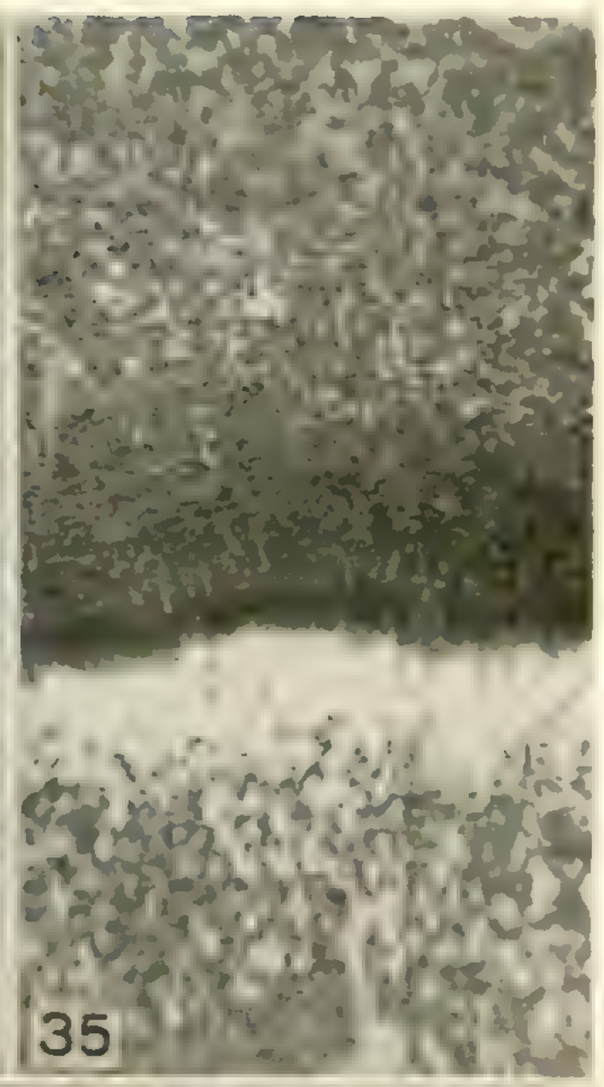

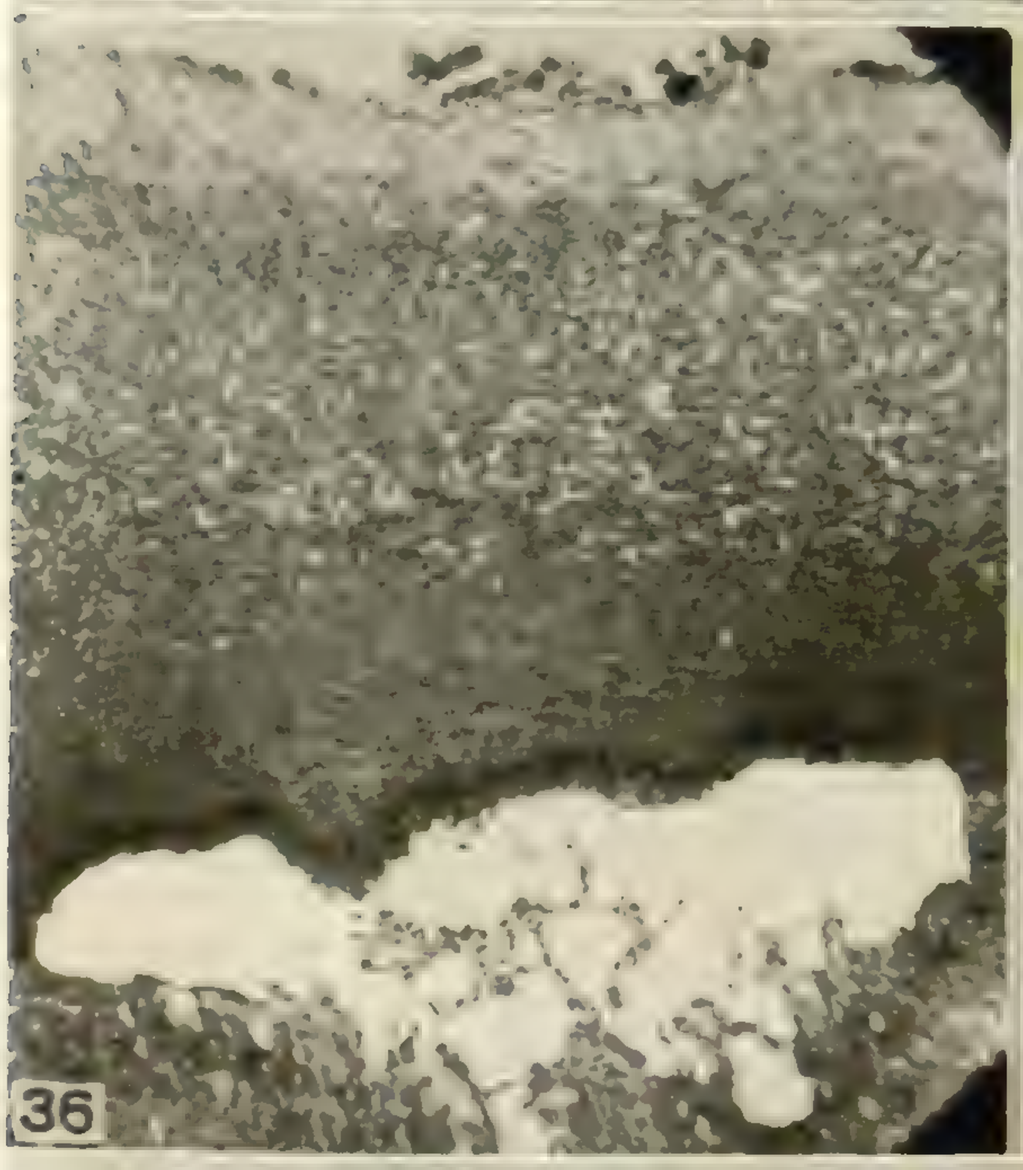

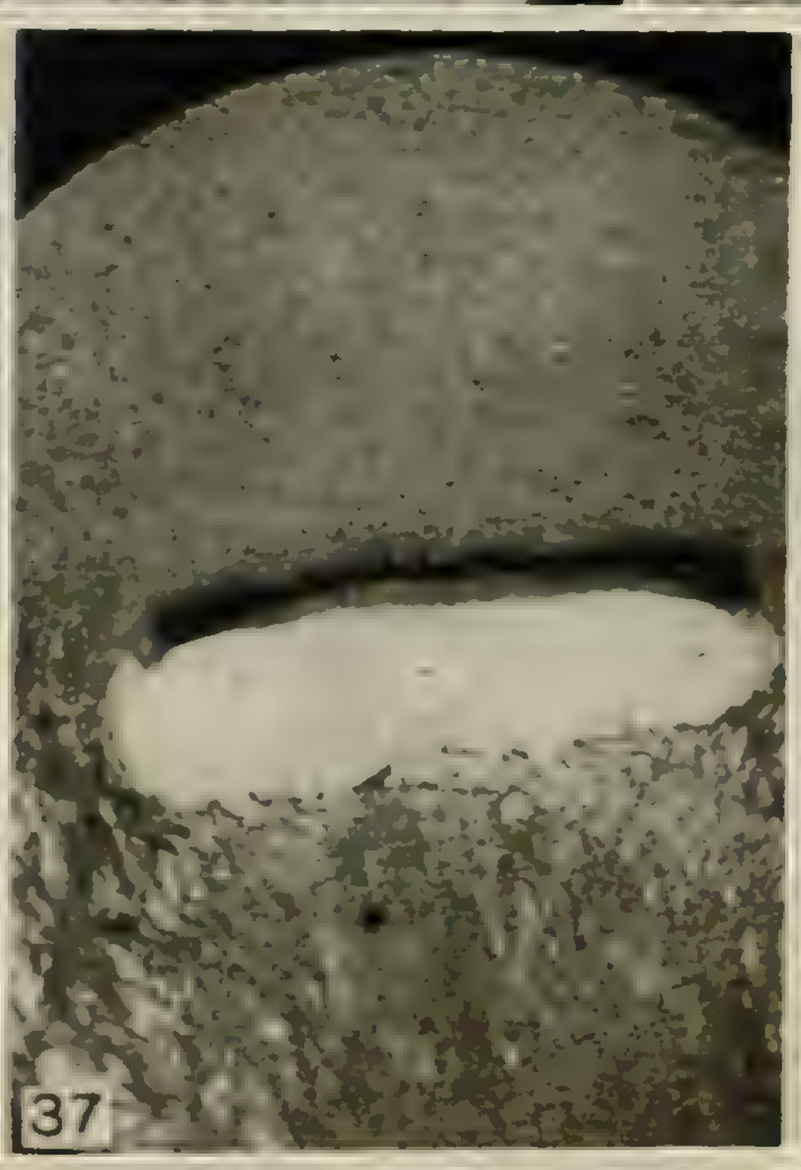

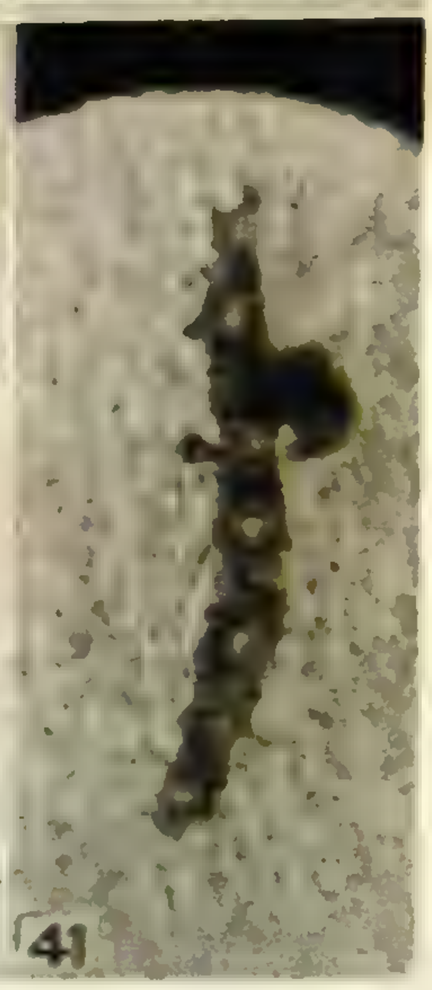

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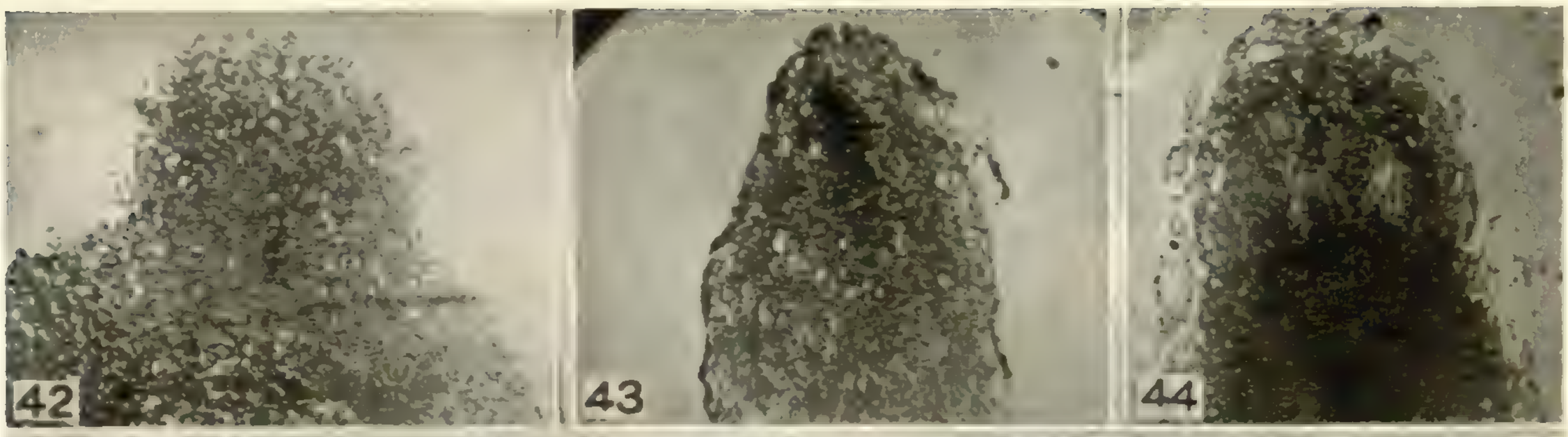

SAWYER on PHOLIOTA

FIG. 50.—Same, nearer stem; note the 3 slight downward projections of palisade, which are very young gill salients; some ground tissue still clings to them because their downward growth relieves tension upon it to some extent; ×67.

FIG. 51.—Section from same fruit body near stem, showing very broad gill salients; ×250

FIG. 52.—Large, thick-walled cells of blematogen; ×250.

FIGS. 53–55.—Sections tangential in enrolled pileus margin; fig. 53 (×33) has not cut into gill cavity; "backs" of gills show as deeper stained areas; in fig. 54 (×154) gill cavity is reached and gill is shown in middle with trama in center and palisade on either side; its origin is in hymenophore both above and below; fig. 55 (×56) is nearer stem.

FIG. 56.—Tangential section, showing well-formed gill, with trama and palisade; ×154.

METHODS OF STUDYING PERMEABILITY OF PROTOPLASM TO SALTS

S. C. Brooks

Investigation of the permeability of protoplasm to electrolytes has led to many apparent conflicts between evidence secured by different methods and between the theoretical conclusions based thereon. An intensive study of the evidence, and of the methods themselves, has shown that these apparent conflicts are in large measure due to an imperfect understanding of the limitations of the methods or to unwarranted assumptions as to the nature and reactions of living matter. It is therefore of interest to consider critically the methods heretofore employed in the study of permeability in order to determine which of these methods may be considered most reliable, and thus to acquire a broader understanding of the problem, and to lay the foundation for further investigation.

The methods employed in the investigation of the permeability of protoplasm to electrolytes fall into 4 general categories, in which the criteria employed are: (1) chemical analysis of tissue extracts or of solutions bathing the tissues, (2) visible changes within the cell, (3) turgidity of cells or tissues, and (4) electrical conductivity of tissues or of masses of cells. To these may be added a diffusion method, which will be described by the writer in a subsequent paper.

Chemical analysis

Analysis of tissues or tissue extracts.—Perhaps the earliest employment of a method for the detection of an inorganic salt within a living cell which had previously been bathed by a solution of that salt was that by Janse (16). Filaments of a species of *Spirogyra* were caused to burst in distilled water containing diphenylamine. Cells which had been bathed in a potassium nitrate solution for some hours previous to testing gave a strong positive reaction in the extruded cell material at the moment of bursting, while those briefly immersed in the potassium nitrate solution, and

then tested, gave no reaction. This method, although positive, can yield only qualitative data.

As a method for the investigation of protoplasmic permeability, quantitative analysis of tissue extracts involves several important sources of error, among which may be mentioned the presence of salts in the intercellular spaces and in the cell walls, where they may be held in solution or by adsorption, variations of the concentration and constitution of expressed juices dependent on the pressure used in extraction (cf. MAMELI **30**), and, most serious of all, adsorption or chemical union of the salts within the cell. Thus, while aluminium ions might displace potassium ions in an adsorption compound, sodium ions might displace the potassium ions to a small extent only. In this way the free aluminium content of the cell would remain low, and the original rate of endosmosis of aluminium salts would be maintained, while that of sodium salts would steadily decrease as the free sodium content of the cell increased. A similar effect might be produced by the formation of hydrates of aluminium and sodium; the former being insoluble would form a precipitate, while the latter would remain in solution.[1] The relative permeability of the tissues to different salts would then be made to appear other than it actually was. The last error also affects methods involving the amount of salt taken by tissues from a solution. Conclusions as to the permeability of the plasma membrane, therefore, cannot be safely based upon data furnished by experiments of this type, such as those of NATHANSOHN (**38**, pp. 453 ff.), PANTANELLI (**51**), DE RUFZ DE LAVISON (**55, 56**), COLIN and DE RUFZ DE LAVISON (**4, 5**), MEURER (**36**), and many others.

PAINE (**50**), using these methods, drew the conclusion that yeast cells are wholly impermeable to inorganic salts.[2] He found a slight absorption of these salts by the yeast cells, but attributed it to adsorption of the salts in the cell walls. Irrespective of the validity of his interpretation, there is no evidence that it is applicable to plants in general.

[1] Precipitates have been observed to form in living cells when they are treated with aluminium salts, but the nature of these precipitates has not been ascertained.

[2] Aqueous solutions of NaCl, $(NH_4)_2 SO_4$, Na_3AsO_4, Na_2HPO_4, and sodium hexose phosphate were used.

ANALYSIS OF SOLUTIONS BATHING THE TISSUES.—The method of analysis may also be applied to the diffusion from living cells ("exosmosis") of substances normally present in the cells and retained by the impermeability of the protoplasm (they may accumulate in the cell walls of terrestrial plants in quantities sufficient to maintain a condition of equilibrium with the solution inside the cell, and may diffuse out when the cells are placed in water). Under certain conditions these substances may be made to diffuse from the cells in appreciable quantities. The experiments of WÄCHTER (**69**) on the exosmosis of sugar from onion bulb scales seemed to indicate that this exosmosis was inhibited by various salts. In the light of more recent evidence it seems possible that this was due to antagonization of traces of toxic salts in the "Leitungs-Wasser" which he used.

Other experiments have dealt with the absorption of salts from the solution as well as with exosmosis. The results of the experiments of TRUE (**63**), TRUE and BARTLETT (**64, 65, 66**), and MERRILL (**34, 35**), like those of WÄCHTER, were visible only after several hours, and the intervening effects upon permeability could not be determined. There was also opportunity for "regulative processes" and other complications to influence the absorption of salts to a marked extent during this interval, and a probability that some of the external cells would be killed and would give off their contained solutes to the surrounding solution. It is quite probable that these effects are of importance in experiments of such long duration as those of the investigators mentioned. The most serious objection to using the analysis of the solution as a criterion of permeability is that the method does not distinguish between permeability and absorption. These two things have little to do with each other. If the absorbed substance is trapped within the cell (by precipitation, or by a chemical change preventing it from diffusing out), it will continue to diffuse in, while a substance which is not trapped will soon stop diffusing in. Hence we see that absorption is no criterion of permeability, although it is so used by many investigators. The absorption of a substance may be great when permeability is small, and vice versa. The same objection applies to some extent to the use of exosmosis as a criterion, since

increased exosmosis may be due, not to increased permeability, but to increased production within the cell of the substance which diffuses out.

Visible changes within the cell

This method, although sometimes valuable in the investigation of the penetration of substances like the alkaloids which form intra-vitam precipitates, and acids and alkalies which cause color changes of pigments or intra-vitam stains, has found little application in the study of the penetration of inorganic salts.

OSTERHOUT (**39**) showed that crystals of calcium oxalate form in the root hairs of seedlings of *Dianthus barbatus* (previously grown in distilled water) within a few hours after their immersion in dilute solutions of calcium salts, and the subsequent normal growth of the cells proved that they were not injured. ENDLER (**7**) followed microscopically the entrance of intra-vitam stains (neutral red and methylene blue) into various plant cells under the influence of various kations. He also investigated the rate of disappearance of the dyes from stained cells, living and dead. The experiments are extremely instructive, showing that at 24 or more hours the passage of dyes through the membrane was increased by kations in the following order: $Na < K < Mg < Ca < Al$. Aluminium formed an exception in that at very low concentrations the exit of dyes from the living cells was inhibited. This inhibition was not observed in the experiments with dead cells, where the influence of the kations was due only to their physical action on the colloidal dye tannate formed in the cells. This series is precisely what would be expected of experiments of long duration on the supposition that a temporary decrease in permeability was produced by all the polyvalent kations, and that this was followed by an increase. Extreme dilution would prolong the period of decreased permeability, and would account for the inhibition of exosmosis which ENDLER found to occur when extremely dilute solutions of aluminium salts were used.

The interesting experiments of LOEB (**29**) on the diffusion of neutral red through the egg membrane of a marine teleost fish (*Fundulus* sp.), a process which occurs readily in electrolyte solutions but very slowly in distilled water, are apparently concerned

with the permeability of a membrane considerably different from the plasma membrane. LOEB suggests the theory that the dye kation is held in the membrane in a combination with a colloidal anion, and that this combination is broken down by the anions of a surrounding salt solution. The behavior of the potassium ion is shown to be like that of the dye kation, at least in its initial stages. Similar processes may occur in the plasma membrane, but it is not possible to apply LOEB's conclusions directly to the behavior of unspecialized protoplasm.

HARVEY (12) has studied the permeability of plant cells to alkalies by introducing an intra-vitam stain, neutral red, which turns yellow in the presence of alkalies.[3] It was found that ammonia and the amines penetrated living and dead tissues with equal and very great rapidity, while the strong bases, although penetrating dead cells with great rapidity, required much longer to penetrate living cells. It seems possible that penetration of bases at the concentration used (0.025 N) was due to injury of the cells.

Turgidity of cells or tissues

The typical living cell behaves toward osmotically active solutions as though it were surrounded by an elastic semipermeable membrane. In view of the widespread confusion regarding the osmotic relations of living cells, it seems necessary to analyze, in so far as the present imperfect state of our knowledge of the physical laws governing osmotic phenomena will allow, the behavior of a cell which acts as a simple osmometer. It will then be possible to judge more accurately the value of the data furnished by the many methods based upon the study of the osmotic relations of living cells. Such a typical cell may be pictured as a body of solution surrounded by an elastic membrane permeable to and bathed by the solvent (in this case water), and slightly if at all permeable to the contained solute. Water will enter such a cell until the internal hydrostatic pressure produced by the tension of the stretched membrane just overcomes the tendency of water to enter the cell. There will thus arise a condition of equilibrium which will be main-

[3] Neutral red changes color between H ion concentrations of 6×10^{-6} and 1×10^{-8} N.

tained unless there is either a change in the tendency of the water to enter, or a change in the tension of the membrane. The latter has not been shown to occur, but may be responsible for certain as yet unexplained phenomena observed in plasmolytic experiments. The former will be produced by alterations in the concentration of the solution bathing the cell, an increase in its concentration causing a loss of water from the cell, with consequent shrinkage, and a decrease causing an intake of water with accompanying increase in volume. These changes will proceed until a new equilibrium is established at which the internal osmotic pressure is again equal to that of the external solution plus the pressure produced by the tension of the membrane.

The rate at which the exchange of water will occur is a function of the difference in osmotic pressure between the intra- and extra-cellular solutions and of the permeability of the membrane to water. There appears to be a tendency among physiologists to confuse the effect of the rate of penetration of a solute on that of water (which is produced by the resultant progressive change in the osmotic gradient), with a hypothetical effect, independent of the osmotic gradient, produced by the simultaneous passage of both solute and solvent through the membrane. There is no physical justification for the latter assumption, and the two ideas should be carefully distinguished. The change in volume of the cell is the sum of the change in volume due to diffusion of water and that due to diffusion of the solute. In cases where the solute is a substance like alcohol, the latter factor may be of considerable importance; but protoplasm is in general so much less permeable to inorganic salts than to water that their diffusion may be neglected in so far as their volume is concerned.

The intra- and extra-cellular osmotic pressures are thus quickly equalized by passage of water through the membrane, and a state of equilibrium is reached, which, if the membrane is permeable to water only, is permanent. But if a diffusion of solute occurs, it will cause changes in osmotic pressure which will lead to further water exchange, and this process will proceed until the solute attains an equal concentration in both intra- and extra-cellular solutions, and a true equilibrium is thus established. The rate at

which these changes occur will depend upon the permeability of the protoplasm to the solute and upon the concentration gradient causing the diffusion of the solute.

If a living cell be placed in a fairly concentrated salt solution, the salt usually diffuses into the cell (a process known as "endosmosis"), while the sugars, to which a large part of the intracellular osmotic pressure was originally due, remain for the most part within the cell. Under these conditions the cell will increase in volume, until it reaches the same turgidity (that is, the same degree of distension due to the tendency of water to enter the cell) which it would have possessed had there been no salt at all present. The outward diffusion of salts or other substances from the cell ("exosmosis") is usually negligible, but it is always to be remembered that such a diffusion may be occurring simultaneously with the endosmosis. If a salt after entering the cell forms there osmotically inactive compounds, either by adsorption or by chemical combination, and does not at the same time cause the liberation of an osmotically equivalent amount of some other substance, the turgidity of the cell is less than would be expected, and there is a decrease in the apparent rate of penetration of the salt.

If a plant cell be placed in a solution which causes shrinkage, the cell wall will contract elastically for a certain distance, and will then suffer no further change in size; meanwhile the continued shrinkage of the protoplasm will cause it to retract from the cell wall. This separation of the protoplasm from the cell wall is known as plasmolysis. It was first observed by PRINGSHEIM (**52**) in 1854, and was ascribed by NÄGELI (**37**) to the impermeability of the protoplast to the plasmolyzing substance. In this process the protoplasm may tear away just inside the cell wall, leaving attached to it a thin layer of protoplasm to which the central mass remains for a time connected by fine threads (cf. BOWER **1**, CHODAT and BOUBIER **3**, HECHT **13**, and KÜSTER **22**). The process of plasmolysis may then subject the protoplasm to a very considerable mechanical injury, and it is quite probable that its subsequent permeability will not be the same as that of a protoplast which has not been subjected to plasmolysis. In animal cells and tissues, where no cell walls are present, and in tissues of plants when shrinkage is not

carried far enough to cause plasmolysis, we have a means of avoiding this objection. We may consider first those methods in which plasmolysis occurs.

METHODS INVOLVING PLASMOLYSIS

1. *Concentration Required to Produce Plasmolysis.*—De Vries (**67**) noticed that the concentration of a glycerine solution just concentrated enough to produce plasmolysis was higher than that expected from the calculated osmotic pressure of the solution. He attributed this to the penetration of glycerine into the cell.

On the assumption that an increase in the concentration of a given substance required to produce plasmolysis indicates an increase of permeability, Lepeschkin (**23, 24, 25, 26**) and Tröndle (**62**) claim to have demonstrated an increase of the permeability of the protoplasm due to increased illumination; and Eckerson (**6**) seeks the cause of the thermotropic curvatures of roots in an increase in permeability due to rise in temperature. By the same method Krehan (**20, 21**) has studied the effect of potassium cyanide on the permeability of cells of *Tradescantia discolor*, the experiments seeming to indicate that dilute solutions (0.001 M) of potassium cyanide cause a temporary and reversible increase in permeability, and that this is followed by a decrease in permeability which begins simultaneously with loss of the reversibility.

Osterhout (**40**) has shown that solutions of sodium and calcium chlorides, either of which alone is unable to produce plasmolysis (of cells of *Spirogyra* sp.), may cause rapid plasmolysis when mixed in such proportions that the ratio of sodium atoms to those of calcium is about 20 to 1. Since the normal permeability of the protoplasm is most nearly attained in the mixed solution, which is a partially balanced mixture, it would appear that the permeability of the protoplasm was abnormally high in one of the pure solutions. It is possible, however, to establish a different interpretation of this phenomenon; this will be considered in the light of evidence secured by other methods.

Fluri (**9**) found that aluminium salts so altered the protoplasm of certain plant cells as to make it impossible to plasmolyze them.

This alteration he supposes to be the production of complete permeability. SZÜCS (**61**) has since stated that the alteration consists of a hardening of the protoplasm, since centrifuging no longer displaces the cell contents. He also found the "hardening" to be temporary, and to be followed by "reliquefaction."

LEPESCHKIN (**27**) claims to determine with great accuracy, by a method based upon the difference in the osmotic pressures of isotonic plasmolyzing substances, the absolute rate of penetration of these substances. It is impossible to explain the method clearly and at the same time briefly, but its essential features are as follows: a comparison of the osmotic pressure of a saccharose solution which will just cause visible plasmolysis, with that of a glycerine solution which, following the saccharose, will cause no change in volume (as determined by LEPESCHKIN'S criterion) shows the latter to be the higher. If we let μ represent a factor proportional to the permeability of the protoplasm to the glycerine, and assume that the protoplasm is impermeable to saccharose, then $\mu = \frac{C^{I} - C}{C^{I}}$, where C^{I} is the concentration of glycerine found to be isotonic with the saccharose solution, and C the concentration calculated to be isosmotic with the saccharose solution. For saccharose we may substitute any substance to which the protoplasm is supposed to be impermeable, and for glycerine any substance whose rate of penetration it is desired to measure.

This method would be exact provided the following assumptions were in accord with the facts: (1) the protoplasm is impermeable to the control substance (in this case saccharose); (2) neither of the substances used causes any alteration in the permeability of the protoplasm; (3) no exosmosis occurs. All these assumptions are rendered highly improbable by the evidence already secured by other methods, and additional evidence against their validity will be submitted by the writer in a subsequent paper.

LEPESCHKIN also appears to assume that there is an effect on the water equilibrium caused by the simultaneous diffusion of solvent and solute through a membrane, and independent of the progressive changes in the osmotic gradient thus arising. This assumption is, as has been previously pointed out, without physical

basis. The method of LEPESCHKIN is therefore of extremely doubtful value.

2. *Recovery from Plasmolysis.*—Recovery of plasmolyzed cells was first noted by KLEBS (17) in 1887, who found that glycerine was able to penetrate the plant cell. He was unable to detect recovery of cells plasmolyzed by solutions of potassium nitrate or sodium chloride. DE VRIES (68) obtained similar results at about the same time. JANSE (16), whose work has been quite generally overlooked, demonstrated the penetration of potassium nitrate, sodium chloride, and saccharose by observations on the recovery of plasmolyzed cells of the marine algae *Chaetomorpha aerea* and *Dictyota* sp., and *Spirogyra nitida*, *Tradescantia discolor*, and *Curcuma* sp. It was thus conclusively shown that at least some inorganic salts can penetrate living cells of many types of plants.

OVERTON (48) was unable to observe any cases of recovery of cells plasmolyzed by inorganic salts. He supposed this to be due to the insolubility of such salts in lipoid substances, which he supposed to constitute the plasma membrane. It has been pointed out by OSTERHOUT (41) that OVERTON in all probability overlooked the recovery of the cells which he used, confusing the subsequent "false plasmolysis," due to the injury of the cells, for a continuation of the true plasmolysis. OSTERHOUT showed that a great variety of salts penetrate and cause recovery. OSTERHOUT also showed that the rate of recovery of *Spirogyra* cells was more rapid when a salt of one of certain monovalent kations was used to produce plasmolysis than when a calcium salt was similarly used.[4] It was impossible to establish more than the most general quantitative relations in these experiments. Recently FITTING (8) has conducted an extensive series of investigations on the permeability of cells of *Tradescantia discolor* L'Heritier (*Rhoeo discolor* Hance). His data may be most easily understood if stated graphically. Comparable strips of epidermis were plasmolyzed in a series of solutions differing by equal increases in molecular concentration. If there was no difference in the rate of recovery, a curve in which the ordinates represented recovery time and the

[4] The solutions used in these experiments were in each case of the lowest concentration which would produce plasmolysis.

abscissae concentration of the plasmolyzing solution would be a straight line. It was found, however, that such a curve was concave to the axis of the ordinates. This indicated a decrease in the rate of recovery with time. FITTING considers this to establish the fact that such salts cause a progressive decrease in the permeability of the protoplasm. He considers the possibility that exosmosis might have occurred in his experiments, and cites experiments which supposedly show that all possible exosmosis had taken place during the preliminary 4–6 hours' exposure of the tissues to distilled water. There are serious discrepancies in his data, such as the fact that a solution of a higher osmotic pressure is required to produce plasmolysis in tissues from which all possible exosmosis is supposed to have taken place than is required to produce it in otherwise comparable tissues from which no exosmosis has occurred. It is probable that FITTING has some important variables in the method which he has employed, and since he has failed to investigate the effect of salts of monovalent kations on exosmosis, it is probable that the supposed decrease of endosmosis is in reality an increase of exosmosis, which would have the same effect on the rate of recovery. FITTING also states that the cells are wholly impermeable to salts of bivalent and trivalent kations, with the possible exception of strontium. This is in conflict with the experiments of OSTERHOUT.

METHODS NOT INVOLVING PLASMOLYSIS

In rapidly elongating plant tissues there is usually a very considerable pressure exerted by the protoplasts against the cell walls which confine them. If all the cell walls of the stem are thin and elastic, the whole stem will be kept in a stretched condition by this pressure. The presence of thick-walled cells, such as fibrovascular or epidermal cells, which do not yield to internal pressure, will, if they are symmetrically distributed, prevent this elongation of the tissue. If we cut such a stem or peduncle so that these two types of tissue are unsymmetrically distributed, the whole tissue will curl so that the elastic tissue forms the longer or convex side. The distention of the elastic tissues, and therefore the degree of curvature, will vary with the turgidity of the tissues. A hypertonic

solution will withdraw water from the cells, and consequently reduce the turgidity and the degree of curvature, while a hypotonic solution will have the opposite effect. The penetration of the protoplasm by a salt with whose solution such a tissue had come into osmotic equilibrium would lead to an increase in the turgidity, and hence in the curvature of the tissue. DE VRIES (**67**), in the investigation of the isotonic coefficients of various substances by this method, observed such a secondary increase in curvature. Such tissue curvatures have not since been used in quantitative researches on the permeability of the protoplasm. The writer, however, has found it possible to make use of this method for quantitative determinations of permeability (BROOKS **1a**).

Changes in the volume or weight of animal cells or tissues have been used by many investigators to determine the rate of penetration of electrolytes. Red blood corpuscles and striated muscle have been the most frequently used materials.[5] As an example of the former, the work of KOZAWA (**19**) may be quoted. This investigator added to 1 cc. of corpuscles centrifuged from defibrinated blood of various mammals 2 cc. of various solutions of equal osmotic pressure (as judged by the freezing point depression). The corpuscles were again centrifuged after a time varying from 15 minutes to 23 hours, and the volume of the mass of corpuscles noted.[6] Increase of volume was considered to indicate penetration of the solute. Sodium salts were not observed to cause any increase in volume. KOEPPE (**18**) made similar observations.

In some animals glucose appeared to penetrate; in others it did not. It was found to be impossible to influence the permeability to glucose by various agents, including certain inorganic salts. These conclusions agree with those obtained by the use of quantitative analytical methods, notably those of GYÖRGY (**10**), who was unable to influence the rate of penetration of glucose into red blood corpuscles by suspension of the corpuscles in buffer solutions of

[5] Changes in weight of whole organisms have been used in the study of osmotic relations. Cf. OVERTON (**48**), QUINTON (**53**), and HENRI and LALOU (**15**).

[6] The determination of volume changes in red blood corpuscles by centrifuging was first suggested by HEDIN (**14**), and is known as the "haematocrit" method. Similar methods have been applied to other free cells such as leucocytes and spermatozoa. Cf. HAMBURGER (**11**).

various hydrogen ion concentrations, or in solutions containing Ca, Mg, Mn, oxalate, or SO_4 ions (cf. also MASING **31** and LOEB **28**).

OVERTON (**49**) made successive determinations of the weight of sartorius muscles of the frog during treatment with various solutions. He reports that no increase in weight took place in a 0.7 per cent sodium chloride solution during a period of many hours; that isotonic solutions of the phosphate, tartrate, sulphate, ethyl sulphate, and acetate of potassium induced no change in weight during 50 hours. After a few hours an increase of weight occurred in solutions of potassium chloride, iodide, bromide, and nitrate, but OVERTON found these changes to be irreversible, and concludes that the normal muscle is impermeable to neutral salts. SIEBECK (**57**), on the other hand, finds that under proper conditions the increase in weight of kidney tissue in a pure isotonic solution of potassium chloride is reversible, and therefore considers that these cells are normally permeable to potassium chloride. In general the permeability of animal cells to neutral salts seems to be less, and more often characterized by selective peculiarities than that of plant cells. The red blood corpuscles, for example, may well be considered to be surrounded by a considerably specialized protoplasmic envelope.

The experiments of LOEB (**29**) on the permeability of fertilized *Fundulus* eggs to electrolytes are concerned with a peculiarly specialized envelope surrounding the embryo. This envelope is characterized by an exceedingly small permeability to salts. Thus an embryo 4–14 days old within the egg membrane survives 3 days of exposure to a solution (50 cc. 3 M NaCl+1 cc. 10/8 M $CaCl_2$) which is almost instantly fatal to the newly hatched fish. As has previously been noted, generalizations as to the permeability of protoplasm cannot be made from data furnished by experiments on such a membrane, and a more extended discussion of the results of these experiments would not be profitable here.

Electrical conductivity of tissues or of masses of cells

The conduction of electrical current by a solution involves the passage through the solution of electrically charged atoms of

some substance. These charged atoms, known as ions, are not created by the electrical conditions imposed, but already exist in all solutions capable of conducting a current. The rate at which the current will be conducted by the ions of a given salt will depend upon two factors, the potential gradient and the frictional or other resistance to the migration of the ions. If the potential gradient be kept constant, we may follow fluctuations in the last factor by a measurement of the current, or by a direct measurement of the electrical resistance. If, therefore, we force the current to pass through living protoplasm in a solution, the resistance offered by the protoplasm to the passage of the ions will measure its permeability to the ions in question (the permeability may be regarded as varying inversely as the resistance). By the use of alternating currents of rather high frequency we avoid large effects due to accumulation of ions at surfaces impermeable to them.[7]

A method of this type was independently employed at about the same time by RÓTH (**54**), BUGARSKY and TANGL (**2**), and STEWART (**58**), who found that the conductivity of blood serum was greater than that of blood itself, and that the resistance rose rapidly with increase of the proportion of corpuscles to serum. The blood corpuscles seemed to be slightly or not at all permeable to the electrolytes of blood. The conductivity of the suspension of corpuscles was shown to be increased by haemolytic agents, the corpuscles then being permeable to salts (cf. WOELFEL **70**, also STEWART **58, 59**). MCCLENDON has also attempted to study the changes in permeability of sea urchin eggs during fertilization (**32**) and of muscles in tetanus (**33**). The evidence from his experiments on sea urchin eggs agrees with that of HARVEY (**12**), previously mentioned, but difficulties in technique which MCCLENDON found it impossible to avoid make the data of these experiments exceedingly unreliable.

The experiments of OSTERHOUT (**42–47**) on the conductivity of tissue of the marine alga *Laminaria* have shown the important fact that the permeability of living protoplasm is altered by salts in pure and mixed solutions in a manner characteristic of the ionic constitu-

[7] The small capacity effect will be proportional to the resistance, so that no relative error is thereby introduced.

tion of the solution. The kations are of particular importance. All monovalent kations (excepting the hydrogen ion) produce only an increase in permeability of the protoplasm. This increase, reversible in its first stages, finally leads to death and complete permeability. Bivalent and trivalent kations and the hydrogen ion cause a temporary and reversible decrease of permeability which is followed or superseded by an increase which is irreversible and leads to death of the cells. In a balanced solution such as sea water the resistance remains constant provided the laboratory conditions are such as to maintain the full vitality of the tissue. We have here a method of determining quantitatively the permeability of the protoplasm at any instant, and the data secured demonstrate the extreme importance of progressive changes in the permeability of protoplasm. It would be possible to imagine that the passage of an electrical current through the tissues was responsible, at least in some measure, for the observed changes in permeability. It would be of advantage, therefore, to check the results of OSTERHOUT'S method by the use of some method entirely free from this possible objection. The method is also applicable to certain types of tissue only, and it is desirable to extend to other types of plants the principles derived by the application of this method.

The plasmolytic experiments of OSTERHOUT (40) may be explained in the light of the experiments by the conductivity method in the following manner. During the time required to produce plasmolysis the permeability has considerably increased in the sodium chloride solution and somewhat decreased in the calcium chloride solution. In that time much more sodium chloride has penetrated the cell, therefore, than of the salts of the mixed solution in which the permeability remains normal, and these again more than the calcium chloride, and the osmotic gradients have changed accordingly. The osmotic pressures of the solutions which will produce visible plasmolysis will then have suffered an increase over the actually isosmotic solutions, and in this order: calcium chloride very little, the mixed solution slightly more, and sodium chloride considerably more. If we now mix a large amount of sodium chloride of a concentration just insufficient to produce plasmolysis with a small amount of a similar calcium chloride

solution, the resulting osmotic pressure will be considerably above that of a similar mixed solution (that is, one just insufficient to cause plasmolysis), and plasmolysis will result.

Summary

From a consideration of the methods heretofore used in the study of permeability it would appear that the steps most essential to further progress toward the solution of the problem are: (1) a thorough analysis of the various disturbing factors in the methods involving chemical determinations and the satisfactory interpretation of the results secured by such methods; (2) the same type of analysis of the methods depending on turgor, with special reference to the possible effect of exosmosis; and (3) the establishment of methods of determining progressive changes in permeability without the various disadvantages of the other methods.

The writer hopes to show in subsequent papers that the diffusion method, which he has devised, answers these requirements, and that it is also possible to interpret satisfactorily the data obtained by certain methods dependent upon the use of turgor as a criterion.

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BRIEFER ARTICLES

NOTES ON EFFECT OF DYES ON *ENDOTHIA PARASITICA*

Some experiments were made in growing the chestnut blight fungus, *Endothia parasitica*, in a liquid medium to which stains had been added. The dyes were congo red, trypan blue, methylene blue, and neutral red plus 7 per cent NaCl, all "vital stains." They were added to a nutrient medium, Pasteur's solution. This solution was not a particularly good one for the cultivation of the fungus. Congo red, trypan blue, and methylene blue were used in 1/1000 of 1 per cent solutions. The dilution of neutral red plus 7 per cent NaCl was not known. This solution had been successfully used in the vital staining of some animals of the lower orders, and it was tried on the fungus by diluting it 1 cc. to 500 cc. of Pasteur's solution. The cultures were started from conidia mixed with a little mycelium taken from a test tube culture.

Record of experiments

CONGO RED (1/1000 of 1 per cent congo red[1] in Pasteur's solution).—Conidia germinated and produced normal mycelium. The hyphae became red colored. When the cultures were 5 days old, hyphae and medium had the same color. Reaction of medium acid to litmus paper. Eleven days after inoculation the medium had turned a pale yellow color, almost colorless, and clear. The medium was acid to litmus paper. The red colored mycelium which had been spreading steadily over the surface of the medium showed in sharp contrast. Seven days later the fully and normally developed fungus had produced pycnidia and conidia. The mycelium in the cultures appeared a pinkish red, and the pycnidia looked yellow. Under the microscope, the color of the hyphae was red to opaque. The colored hyphae turned blue at once on being placed in $\frac{1}{3}$ per cent sulphuric acid and later lost their color. The pycnidia on being tested in sulphuric acid varied in reaction; some of them turned blue, some did not. The conidia in the crushed fruits showed no color.

TRYPAN BLUE (1/1000 of 1 per cent trypan[2] blue in Pasteur's solution).—All the conidia stained a deep blue, so that their growth could

[1] G. Grübler and Company.

[2] Meister Lucius and Brüning Hoechst.

be followed readily. They swelled, germinated, and produced normal mycelia. The hyphae were a deep blue; the growing tips were opaque to pale blue. Their blue color deepened with age. About 12 days after inoculation the medium lost its blue color, turning light yellow; the blue hyphae with uncolored pycnidia floated on its surface.

METHYLENE BLUE (1/1000 of 1 per cent methylene blue[3] in Pasteur's solution).—The majority of conidia did not germinate, but instead developed vacuoles. The hyphae produced did not stain, except when the cells were dead. The plasmolyzed contents of the dead cells gathered in a blue clump in the center. These isolated dead cells distributed throughout the mycelium gave it a pale blue color. While the cultures grew more vigorously than the controls, they did not grow as well as the congo red and trypan blue cultures. No fruits were produced.

NEUTRAL RED (neutral red plus 7 per cent NaCl solution diluted 1 to 500 parts Pasteur's solution).—A few conidia germinated and grew. The cultures were as good as the controls. No fruits. Hyphae uncolored.

CONTROL (Pasteur's solution).—Conidia germinated, produced mycelium, but no pycnidia.

In the case of the congo red and trypan blue cultures, it was thought that the mycelium had gradually stored up all the dye in the medium. Neutral red and salt did not stain. In those cases in which methylene blue penetrated the cells, it apparently was fatal. The fact that the solutions containing the stains supported the fungus better than the control medium seems to indicate one of two things: either the toxicity of the dyes in the concentrations used (with the exception of the neutral red and salt) was enough to be a stimulus, or the dyes may have counteracted the elements in Pasteur's solution inhibitive to the growth of the fungus and so allowed the mycelium a better development.

PFEFFER,[4] in a series of experiments with methylene blue, found the dye accumulated in the cell sap rather than in the protoplast of the cell. The substances which render the storage possible, he says, are not always identical; the two which are best known are tannin and phloroglucin. Mycelium taken from cornmeal agar cultures was tested for the presence of tannin and phloroglucin. There was no evidence of these two substances in the vegetative cells. The reagents used were ferric sulphate, hydrogen peroxide and ferrous sulphate, copper acetate, ferrous sulphate, and boiling potassium bichromate.

[3] G. Grübler and Company.

[4] PFEFFER, W., Untersuchungen Botanischen Institut zu Tübingen. 1886. II.

Mycelia growing in a congo red 1 to 200 parts maltose solution were examined to see whether the dye had accumulated in the vacuoles or protoplast of the cell. The mycelium had not behaved with methylene blue as with the two colloids, but this gave no indication as to the deposition of the pigments.

The fungus grew in the solution, but not vigorously. The mycelium was so deeply stained as to be reddish black. Under the microscope the conidia and older cells of the hyphae were dark red, while the youngest cells were a pale pink. Treatment with 50 per cent nitric acid showed by its blue colored reaction that most of the pigment was in the walls of all the cells, only less in the younger cells. The hyphae were plasmolyzed with a NaCl solution and also by drying; the contracted protoplasm in the center of the cells was red, the cell wall looking white in contrast. This first was noticed in the younger cells, the quantity of pigment in the older cell walls having obscured the color of the protoplast, until the last stages of plasmolysis had been reached. Sulphuric acid, nitric, or hydrochloric produced besides a blue color, what was thought might be a blue precipitate. These very small spots, seen with the oil immersion lens, were on the cell walls and inside on the plasmolyzed protoplast. Glycerin caused the color to stream from the mycelium. Sodium hydroxide, while it brightened the red, also caused the color to diffuse into the surrounding solution. Throughout all these reactions glistening white granules in the protoplasts could be seen.

It would seem from these reactions that a great deal of the congo red accumulated in the cell walls, some passed inside the cell walls, where it appeared as though the protoplast had stored the dye in the form of minute granules. In the nutrient solutions containing congo red, the difference in the ability of fungi to store stain was so marked that contaminations could be seen at once. For instance, *Penicillium* sp., yeast, and a rod-shaped bacterium found growing in them remained unstained until dead.

It is suggested that *Endothia parasitica* (Mur.) A. and A. may be a good subject for the study of mitochondria in fungous cells.—CAROLINE RUMBOLD, *Botanical Laboratory, University of Pennsylvania.*

CURRENT LITERATURE

BOOK REVIEWS

The study of plants

WOODHEAD[1] has published an elementary textbook of botany which seems to possess several features deserving better things than this tardy notice. It is a pleasure to note that emphasis is placed upon the work of plants and their relation to the habitat. Form is considered in relation to function, and the amount of microscopic work is reduced to a minimum. The book is divided into 5 parts, the first being devoted to the structure and function of the vegetative organs, occupying 150 pages. About half as much space is devoted to the reproductive organs, and here, as before, attention is confined to seed plants. The next 100 pages contain a characterization of the great groups of systematic botany, including a special consideration of trees and shrubs. The final portion is an introduction to the study of plant communities, including those of the roadside and cultivated fields. One of the commendable features of the book is the choice of so much material from the common plants of the field and wayside. It is a relief to see such a large number of new illustrations, including some good photomicrographs replacing the stock figures that reappear so persistently in most textbooks.

The final chapters are well organized to introduce the concepts and principles of plant associations, and possess the further advantage that the examples are chosen from the vegetation of the British Isles, thus affording an opportunity of following principles involved rather than copying directly the lessons outlined in the text. This among other things will certainly make the book indispensable to the teacher in search of new ideas and fresh exercises with which to enliven his present program.

It would not be difficult to find points to be criticized, but they are not on the whole serious defects. As an example, there is the use of "abnormal forms" to describe roots that are not of the most common fibrous type. The difference in the terminology from that commonly used in this country would probably be a serious difficulty in introducing it as a text for class use, but as a book of secondary reference and as a source of different ideas and new material it should not be overlooked.—GEO. D. FULLER.

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[1] WOODHEAD, T. W., The study of plants; an introduction to botany and plant ecology. 8vo. pp. 424. *figs. 258*. Oxford: Clarendon Press. 1915. $1.40.

The life of inland waters

This book[2] attempts to present in an elementary manner a comprehensive view of our fresh waters as the abode of a teeming multitude of organisms. The viewpoint is essentially ecological, with a background of economic possibilities. The first portion of the volume consists of an introduction to the subject, that is to the science of limnology, including a historical sketch of important epochs in its development and a glance at the present facilities for study, which include some 30 biological field stations in the United States and Canada. There follows a discussion of water with respect to its transparency, temperature, and circulation, as well as its gas, mineral, and organic content. The various types of aquatic habitats are then presented. These include ponds, lakes, streams, marshes, and bogs.

In the consideration of aquatic organisms, 57 pages are devoted to plant and 83 to animal forms. Concerning the latter the reviewer will venture no opinion, but the paragraphs on plant life seem interesting and accurate, but so general that they would need to be supplemented by good teaching in the field to accomplish their purpose. In such an ecological textbook the adjustment of organisms to the varied conditions of aquatic life under which they exist, and the interaction of the aquatic communities are, of course, the most important parts of the book, and considering the immensity of the field to be covered and the complexity of the material it would seem that the authors have been very successful. Still the book will have to be supplemented by a teacher with an unusually wide acquaintance with both plant and animal life in order to be the success which the subject deserves.

The final chapter upon the possibilities of water crops and water culture reveals economic possibilities of no small importance. The entire volume is in non-technical language, the material is well organized, and the contents may be appreciated by a person with a minimum of scientific attainment, while at the same time few teachers will find themselves sufficiently equipped to teach the entire field effectively. Good illustrations and a fairly extensive bibliography add to the value of the volume.—GEO. D. FULLER.

MINOR NOTICES

Fruit diseases.—A recent textbook by HESLER and WHETZEL[3] discusses the subject from an essentially New England viewpoint, omitting from all consideration fruits and diseases that are of major interest in many states and nearly all that are of interest in our tropical possessions. The discussion of such diseases as are treated is in many instances from a local viewpoint rather

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[2] NEEDAM, JAMES G., and LLOYD, J. T., The life of inland waters. 8vo. pp. 438. *figs.* 244. New York: Comstock Co. 1916. $3.00.

[3] HESLER, LEX R., and WHETZEL, HERBERT RICE, Manual of fruit diseases. 12mo. pp. xx+462. *figs.* 126. New York: Macmillan. 1917.

than of a general nature. This is especially obvious in the treatment of such diseases as apple rust and pear blight. The illustrations are poor. Such figures as 29, 32, 40, 69, 76, 83, 86, 92, 98 are not worthy of publication. Throughout the book there is a tendency to present various conflicting theories and arguments concerning a given disease, with the result that often the real conclusions, if any, are buried or obscured. This really is the result of the status of pathology, of insufficient knowledge of the diseases in question, but the value of such presentation to the student and especially to the practical grower is doubtful. Assuming a central New York viewpoint and interest, the book may be said to give a very complete presentation of what is known of fruit diseases, with valuable lists of references to original sources of information. It is, as the authors announce, the first American text to deal wholly with diseases of fruits, and here for the first time are brought together with comprehensive discussion many obscure and little-known diseases. The facts presented are well selected, and the book constitutes a valuable addition to the literature of plant diseases. —F. L. STEVENS.

North American Flora.—The second part of Vol. 21 contains the presentation of Amaranthaceae by STANDLEY,[4] who recognizes 166 species distributed among 21 genera. *Amaranthus* is much the largest genus, with 42 species, followed by *Iresine* with 32, *Achyranthes* with 31, and *Gomphrena* with 15. These 4 genera contain 120 of the 166 species, the remaining 46 being distributed among 17 genera. New species, 10 in number, are described in *Amaranthus* (4), *Acnida*, *Froelichia*, *Achyranthes*, *Gomphrena* (2), and *Iresine*.—J. M. C.

North American Flora.—The second part of Vol. 10 contains the presentation of Agaricales by MURRILL,[5] including the subtribe Pluteanae. The largest genera are *Entoloma* (63 spp.), *Pluteus* (57 spp.), and *Leptoniella* (43 spp.). Ten genera are presented, and 109 new species are distributed as follows: *Claudopus*, *Eccilia* (9), *Leptoniella* (14), *Nolanea* (11), *Pleuropus* (7), *Entoloma* (34), *Pluteus* (30), *Chamaeota*, and *Volvariopsis* (2).—J. M. C.

NOTES FOR STUDENTS

Anthocyans.—Since the review of the anthocyan (anthocyanin) pigments by CROCKER,[6] much of interest from the chemical point of view has appeared. As pointed out by CROCKER, these facts are of marked significance to all botanists. Students interested in the general problems of anthocyans (botanical, chemical, and genetic) will find much of value in Miss WHELDALE's book.[7]

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[4] STANDLEY, PAUL C., North American Flora **21**:part 2. pp. 95–169. (Chenopodiales) Amaranthaceae. New York Botanic Garden. 1917.

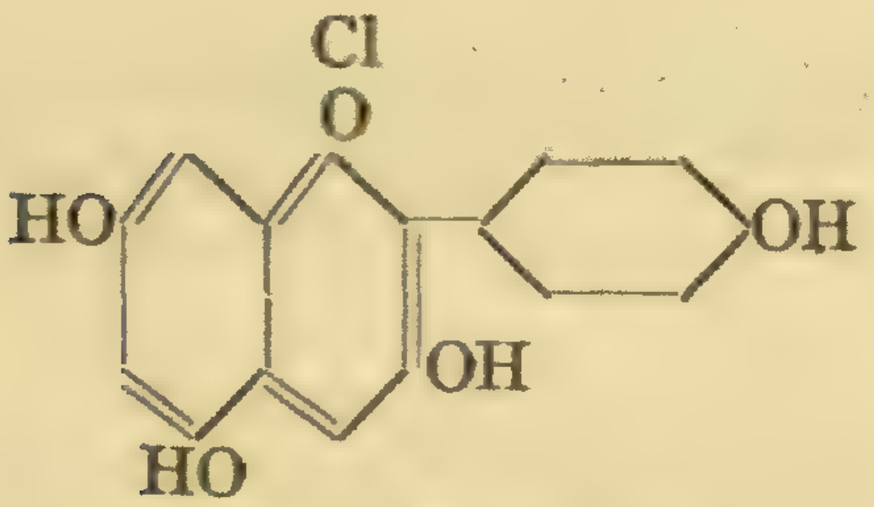
[5] MURRILL, W. A., North American Flora **10**:part 2. pp. 77–144. Agaricales: Agaricaceae (pars); Agariceae (pars). New York Botanic Garden. 1917.

[6] CROCKER, WM., BOT. GAZ. **61**:349. 1916.

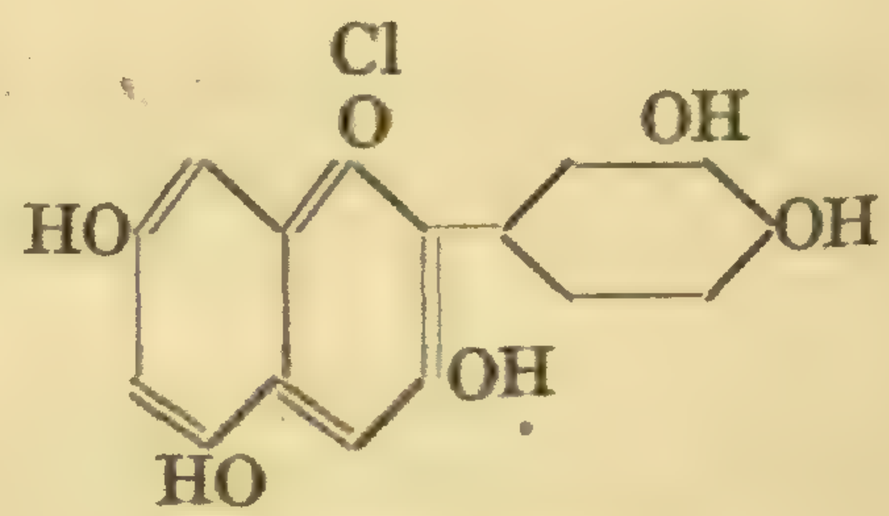
[7] WHELDALE, M., The anthocyanin pigments of plants. Cambridge University Press. 1916.

The bibliography is very complete and should stimulate further work. Brief reviews of the anthocyan pigments have recently appeared by ATKINS,[8] EVEREST,[9] WHELDALE,[10] TRUTTWIN,[11] and WEST.[12]

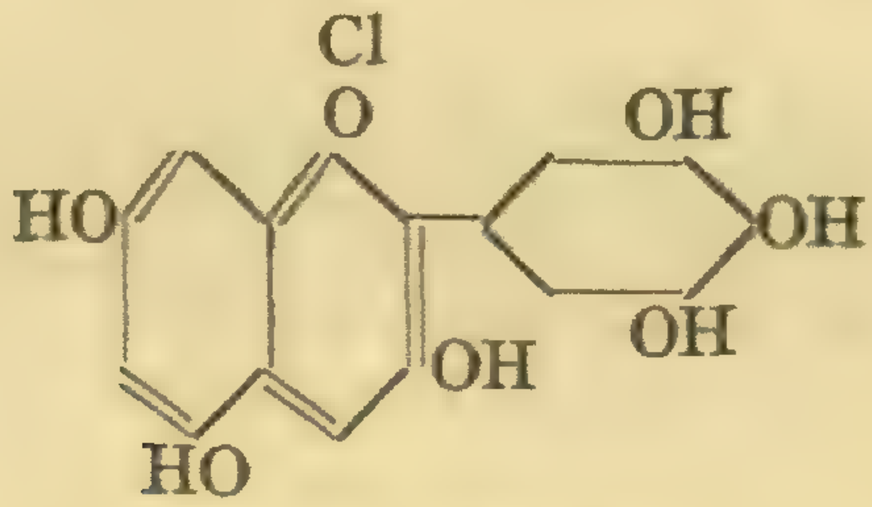
The constitution of the anthocyanidins (the sugar-free compound, obtained upon hydrolysis of the anthocyan with 20 per cent hydrochloric acid) has been definitely established by the synthesis of cyanidin (by the reduction of quercetin with magnesium at 35°),[13] and of pelargonidin (in which phloroglucinic aldehyde was the starting point).[14] These syntheses prove the correctness of the formulas earlier proposed by WILLSTÄTTER, after studying the physical and chemical properties of the anthocyanidin chlorides. The mechanism of the reduction of quercetin and other flavones to anthocyanidins has been questioned by certain Japanese workers,[15] who claim to have isolated various magnesium compounds as intermediate products. These criticisms, however, in no way invalidate the general conclusion as to the structure of the anthocyanidins.



Pelargonidin chloride



Cyanidin chloride



Delphinidin chloride

[8] ATKINS, W. R. G., Researches in plant physiology. Whittaker Co. 1916.

[9] EVEREST, A. E., Science Progress **9**:597. 1914–15; Jour. Genetics **4**:367. 1914–15.

[10] WHELDALE, M., Jour. Genetics **4**:109, 369. 1914–15.

[11] TRUTTWIN, HANS, Chem. Zeit. **40**:478. 1916.

[12] WEST, CLARENCE J., Register of Phi Lambda Upsilon **6**:1–18. 1917.

[13] WILLSTÄTTER, R., and MALLISON, H., Sitz. Ber. Akad. Wiss. **12**:769. 1914.

[14] WILLSTÄTTER, R., and ZECHMEISTER, L., Sitz. Ber. Akad. Wiss. **12**:886. 1914.

[15] SHIBATA, K., SHIBATA, Y., and KASIWAGI, I., Jour. Pharm. Soc. Japan no. 417. 1916; Chem. Abstr. **11**:578. 1917.

The amyl alcohol test for anthocyans has played an important part in the course of WILLSTÄTTER'S work. The anthocyan (glucoside) remains quantitatively in dilute (2 N) sulphuric acid when shaken with amyl alcohol, whereas the anthocyanidin (non-glucoside) passes quantitatively into the alcoholic layer, yielding a red solution. When shaken with a solution of sodium acetate the red color becomes violet or violet red, the pigment remaining quantitatively in the amyl alcohol. On shaking with sodium carbonate, the alcohol solution turns blue or bluish-green, and at the same time the pigment descends quantitatively into the aqueous layer.

This is true only for diglucosides. Monoglucosides yield a certain amount of the pigment to the amyl alcohol. Rhamnose glucosides (containing one molecule each of rhamnose and glucose) behave like the monoglucosides. From this it is seen that the test may be used to distinguish nomo- and rhamnose-glucosides from diglucosides.

The test is also of service in testing the individuality of anthocyan. For this the acid used must be of sufficient concentration to prevent the conversion of the colored chloride into the colorless carbinol (ψ base) and yet must be dilute enough to dissolve the chloride readily (0.5 per cent hydrochloric acid is recommended). The solutions must be very dilute on account of the limited solubility of the coloring matter in amyl alcohol. The intensity of the color of the amyl alcohol solution is compared with that of the anthocyan chloride. Two successive extractions with amyl alcohol are made, and the fraction of the anthocyan in the extracts, called the "partition number," should be the same in both cases.

WILLSTÄTTER'S first work indicated that the flower and fruit pigments might fall into 3 classes, depending upon whether the sugar-free component was pelargonidin, cyanidin, or delphinidin. The possibility of the other classes was not excluded, but they were not found. The second series of papers would seem to confirm this.[16] Here, also, only pigments belonging to one of these three classes were found. It is true that the possibility of other classes is, again, not excluded. Indeed, WILLSTÄTTER states in the article on the poppy that the preliminary work on different varieties of this flower has indicated that the isolation of several new anthocyanidins may be expected. The one flower studied, however, was found to contain cyanidin.

Table I gives the pigments thus far isolated and studied, together with the formula of chloride, the source from which it was isolated, the anthocyanidin resulting on hydrolysis and the sugar component. They are divided into the 3 classes mentioned.

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[16] WILLSTÄTTER, R., Untersuchungen über die Anthocyane. XI (with BOLTON, E. K.). Ann. **412**:113. 1916; XII (with BOLTON, E. K.). *Ibid.* 136; XIII (with BURDICK, C. L.). *Ibid.* 149; XIV (with ZOLLINGER, E. H.). *Ibid.* 164; XV (with WEIL, F. J.). *Ibid.* 178; XVI (with ZOLLINGER, E. H.). *Ibid.* 195; XVII (with BURDICK, C. L.). *Ibid.* 217; XVIII (with WEIL, F. J.). *Ibid.* 231.

The relationships of these various anthocyans and anthocyanidins may best be seen from the diagrams on page 259.

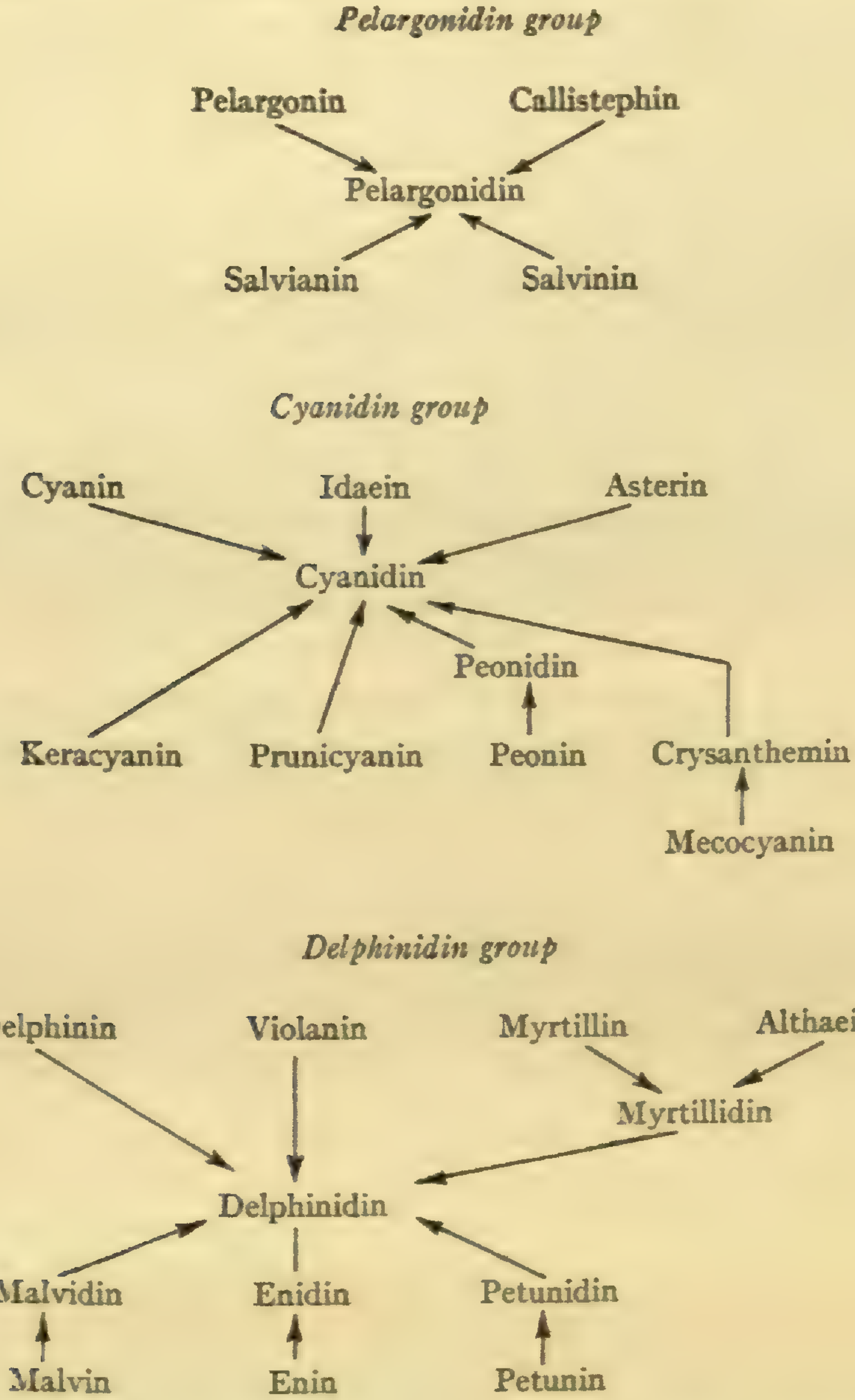
TABLE I

Anthocyan	Formula	Anthocyanidin	Occurrence	Sugar components
Pelargonidingroup				
Pelargonin	$C_{27}H_{31}O_{15}Cl$	Pelargonidin	Scarlet red pelargonium, cornflower, orange red and dark violet dahlia	2 glucose
Callistephin....	$C_{21}H_{21}O_{10}Cl$	"	Summer aster	1 "
Salvianin.....	.....	"	Scarlet red salvia	2 "
Salvinin.....	$C_{27}H_{31}O_{15}Cl$	"	Salvia	2 "
Salvin.....	$C_{27}H_{27}O_{13}Cl$	"	Salvia	
Cyanidin group				
Cyanin.....	$C_{27}H_{31}O_{16}Cl$	Cyanidin	Cornflower, rose, dark red garden dahlia	2 glucose
Idaein.....	$C_{21}H_{21}O_{11}Cl$	"	Whortleberry	1 galactose
Chrysanthemin	$C_{21}H_{21}O_{11}Cl$	"	Chrysanthemum	1 glucose
Asterin.....	$C_{21}H_{21}O_{11}Cl$	"	Summer aster	1 "
Keracyanin....	$C_{27}H_{31}O_{15}Cl$	"	Cherry	Glucose and rhamnose
Prunicyanin...	$C_{27}H_{31}O_{15}Cl$	"	Black thornberry	Rhamnose and a hexose
Mecocyanin....	$C_{27}H_{31}O_{16}Cl$	"	Poppy	2 glucose
Peonin.....	$C_{28}H_{33}O_{16}Cl$	Peonidin*	Peony	1 "
Delphinidin group				
Delphinin.....	$C_{41}H_{39}O_{21}Cl$	Delphinidin	Larkspur	2 "
Violanin	.....	"	Pansy	Rhamnose and glucose
Enin.....	$C_{23}H_{23}O_{12}Cl$	Enidin*	Grapes	1 glucose
Malvin.....	$C_{29}H_{35}O_{17}Cl$	Malvidin*	Wild mallow	2 "
Myrtillin.....	$C_{23}H_{23}O_{12}Cl$	Myrtillidin*	Bilberry	1 "
Althaein.....	$C_{22}H_{23}O_{12}Cl$	" *	Hollyhock	1 "
Petunin.....	$C_{28}H_{33}O_{17}Cl$	Petunidin*	Petunia	2 "
Ampelopsin....	$C_{22}H_{23}O_{12}Cl$	Ampelopsidin*	*Ampelopsis* (wild grapes)	1 "

*Mono—or dimethyl ethers.

A study of table I shows the remarkable distribution of each group. Thus, cyanidin glucosides have been isolated from the following sources: the blue corn flower contains 0.7 per cent of the dry weight of the flower, while the Bordeaux red variety contains 13–14 per cent; 2 per cent of the dry weight of the rose (commercial *Rosa gallica*) and 20 per cent of the dark red garden dahlia are cyanin. Cyanidin has also been isolated from the chrysanthemum, the summer aster, the poppy, and the peony. Varying amounts of cyanidin glucosides are found in the following: *Zinnia elegans* Jacq., *Gaillardia bicolor* Hook., *Helenium autumnale* L., *Gadiolus* (the scarlet varieties of which contain a pelargonidin glucoside), *Tulipa Gesneriana* L., *Tropaeolum majus* L., *Ribes*

rubrum L., the raspberry, and the berry of the mountain ash. These glucosides also occur very extensively in fruits and in yellowish red, red, brown, and dark blue berries. They have been isolated from the cranberry, the cherry, the sloe (black thornberry), and the plum. The occurrence of a pure red coloring



matter in the bluish black skins of such fruits is remarkable. Some explanation has to be found as to how cyanidin is able to impart such deep colors to fruits. The other groups show almost as wide a distribution as does the cyanidin group.

The conclusion that the color of the flower depends, in part, upon the reaction of the cell sap seems to need some modification, in view of the work of

HAAS[17] on this question. Determination of the total acidity and actual acidity by means of titration, and the gas chain and buffer solutions, shows that the reaction of the cells studied ranges from about P_H+3 to P_H+7. If we call the buffer solution acid up to P_H+7, neutral when at P_H+7, and alkaline when higher than P_H+7, it is evident that it is unsafe to call cell sap acid when red, neutral or alkaline when blue, and markedly alkaline when green, unless the color changes of the particular pigment are first studied by some method, such as that of using buffer solutions of known hydrogen ion concentration.

One other study may also be mentioned in this connection. These chemical investigations inspired a study by SHIBATA, NAGAI, and KISHIDA[18] of the physiological and biological significance of the anthocyans and flavones in plants. The evidence obtained established a somewhat unexpected fact, namely, that the flavone derivatives are one of the cell contents of very common occurrence in the plant kingdom. In fact, they are quite as common as chlorophyll, tannins, sugars, starches, and proteins. They are not only found in the yellow coloring matter, but also in the cell sap of the epidermis and in the underlying tissue of plants in general. In only a small number of plants is a complete absence of chromogen proved; for example, in the white corn flower (*Centaurea cyanus*), oxalis (*Oxalis violacea*), pink (*Dianthus caryphyllus*), and pelargonium (*Pelargonium cucullatum*). The function of the flavone derivatives dissolved in the cell sap is to protect the living protoplasm and the important biochemical agents involved from the injurious action of the ultraviolet rays of sunlight by absorbing them at the peripheral layer of the plant organism. The plausibility of this assumption is justified by an extensive study of the flora of alpine and tropical regions. The green leaves of deciduous trees, which produce anthocyan pigments in autumn, contain a considerable amount of flavones. The production of autumnal color is due to the biochemical change, that is, the reduction of already existing flavones in the leaf, initiated by the physiological condition at the end of the growing season, without having special ecological significance.

This brief survey of recent progress in anthocyan chemistry makes it seem very probable that in the near future we may have a complete classification of these pigments, based upon accurate and definite knowledge of the chemical structure of the substances involved. It is to be hoped that the work may make substantial progress in spite of the war.—CLARENCE J. WEST.

Taxonomic notes.—EVANS[19] has published a monograph of the North American species of *Marchantia*, recognizing 9 species, one of which (*M. breviloba* of Jamaica) is new. The extensive discussion of species is preceded

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[17] HAAS, A. R., Jour. Biol. Chem. **27**:233. 1916; BOT. GAZ. **63**:232. 1917.

[18] SHIBATA, K., NAGAI, I., and KISHIDA, M., Jour. Biol. Chem. **28**:93. 1916–17.

[19] EVANS, ALEXANDER W., The American species of *Marchantia*. Trans. Conn. Acad. Sci. **21**:201–313. *figs. 20*. 1917.

by an account of the morphology of the genus. The detailed description of each species is accompanied by the synonymy, citations of exsiccatae, and a very full discussion.

In a revision of *Herberta*, the same author[20] discusses 4 species, 2 of which are described as new.

FERNALD[21] has described a new *Cardamine* (*C. Longii*) from Maine, which grows in "shaded rock-pockets and crevices covered at high tide." In the description it is contrasted with *C. pennsylvanica*.

MACKENZIE[22] has described a new species of *Carex* (*C. convoluta*), which ranges from Maine to Manitoba and south to the Gulf States. Heretofore it has been included in *C. rosea*.

PENNELL,[23] in continuation of his studies of the plants of the southern states, has described a new *Smilax* (*S. leptanthera*) from Georgia, closely allied to *S. tamnifolia*.

RENDLE[24] has described a new genus (*Maidenia*) of Hydrocharidaceae from West Australia, belonging to the Vallisnerieae.

ROCK,[25] in connection with the preparation of a monograph of certain genera of the Lobeliaceae of Hawaii, has published 9 new species and varieties of *Cyanea*, and 2 new varieties of *Lobelia*.

WIEGAND[26] has described a new species of *Eragrostis* (*E. peregrina*), which occurs as a weed in this country, as well as in Germany and Japan, and which is unknown as yet in an indigenous state. It was separated from the well known *E. pilosa* of Europe and America, and had been named *E. pilosa* var. *condensata* Hackel.—J. M. C.

A peculiar spore distribution.—According to ROMELL,[27] the brown powder commonly observed covering the upper surfaces of sporophores of

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[20] EVANS, ALEXANDER W., Notes on the genus *Herberta*, with a revision of the species known from Europe, Canada, and the United States. Bull. Torr. Bot. Club **44**:191–222. *pl. 8.* 1917.

[21] FERNALD, M. L., A new *Cardamine* from southern Maine. Rhodora **19**:91, 92. 1917.

[22] MACKENZIE, K. K. Notes on *Carex*. X. Bull. Torr. Bot. Club **43**:428. 1916.

[23] PENNELL, F. W., Notes on plants of the southern United States. II. Bull. Torr. Bot. Club **43**:412. 1916.

[24] RENDLE, A. B., *Maidenia*, a new genus of Hydrocharidaceae. Jour. Botany **54**:313–316. *pl. 545.* 1916.

[25] ROCK, JOSEPH F., Notes on Hawaiian Lobelioideae, with descriptions of new species and varieties. Bull. Torr. Bot. Club **44**:229–239. *pls. 9–16.* 1917.

[26] WIEGAND, K. M., A new species of *Eragrostis*. Rhodora **19**:93–96. 1917.

[27] ROMELL, LARS, Hvarifrån kammer det Bruna Pulvrit å öfre Sidan af *Polyporus applanatus* och andra *Ganoderma*-arter? Svensk. Bot. Tidskr. **10**:340–348. 1916 (with English summary).

some species of *Fomes* consists of true basidiospores which have been carried upward by gentle currents of air, such as arise from differences of temperature at different levels, and have lodged on the pilei. In support of this view the author points out that other objects in the vicinity of the fungi also become covered with spores. A simple experiment lends further support to this view. Pieces of cardboard pinned on the surface of sporophores of *Polyporus applanatus* in May were covered with spore powder in July, as were also all portions of the surfaces of the fruit bodies except the areas covered by the paper. While not venturing to explain the pertinaceous adherence of the spores to surfaces, the author suggests that they stick fast by virtue of a gelatinous cutin layer. Regarding the spore powder on the surface of these fungi, mycologists have generally adopted the view of SCHULZER, according to which the powder consists of conidia whose origin on the surface of the pileus is minutely described by him. Although opposing the view of SCHULZER, ROMELL does not speak of repeating the histological examination of that investigator. If the explanation of ROMELL is correct, it is a matter for inquiry why this peculiarity of spore distribution is restricted to a few members of the genus *Fomes* and does not occur more generally among the Hymenomycetes. Even among the caespitose Agaricaceae, only those parts of the pilei overtopped by others are usually covered by spores, while the exposed parts generally remain free.—H. HASSELBRING.

Journal of Forestry.—With the issue of January 1917 the *Journal of Forestry*[28] takes the place of the *Proceedings of the Society of American Foresters* and of the *Forestry Quarterly*. This change is in no sense an absorption of either journal by the other, but rather an amalgamation of the best features of the two original publications is intended. In continuing the activities of the two parent publications it is expected that the new one will contain 800 to 1200 pages per annual volume.

The first number of the new journal sets a high standard of excellence which promises well for its future. Among its leading articles is a critical review of 30 years of forestry work of the Federal Government by FERNOW. Some slight idea of the progress involved may be formed from the increase in appropriations from $10,000 in 1886 to over $5,000,000 at present. In addition to the Federal organization, 30 states have organized forest departments and 13 now possess state forests. There is also a thorough discussion of "continuous forest production of privately owned timberlands" by KIRKLAND, and an excellent critical review of recent papers on the moisture withholding power of soils by MOORE. Perhaps still more useful to botanists and ecologists is an extended glossary of the technical terms of forestry now used by the profession in America.

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[28] Journal of Forestry. 8 monthly issues per year. Pub. by the Society of American Foresters. Washington, D.C. $3.00 per year.

It is safe to predict that the new journal will be of increasing interest to all botanists, and more particularly so to ecologists who see in forestry the practical application of their more theoretical studies.—GEO. D. FULLER.

Endemism and the mutation theory.—WILLIS, in papers previously reviewed in this journal,[29] working upon the flora of Ceylon, has proposed the theory that relative endemism is determined by relative age, the youngest species being the endemics. RIDLEY[30] points out that WILLIS has based his arguments upon statistics gathered from herbarium specimens; and illustrates that such will not agree with field statistics, the commonest species sometimes being poorly represented in the herbarium. In connection with his theory WILLIS states that "very common" plants could not disappear without a geological catastrophe. This RIDLEY has shown to be inaccurate, illustrating from his own personal experience and from well known historical evidence that common species have disappeared within a few years, due to parasites, the activities of man, and relatively slight climatic changes. RIDLEY claims that the Ceylon endemics are relics, since there are no other local species from which they could have been evolved recently.

The remainder of the paper is a criticism of the mutation theory as used by WILLIS to explain the origin of the Ceylon flora. RIDLEY's arguments and evidence are of the characteristic Neo-Darwinian type. As an attack upon the mutation theory, or WILLIS' application of it, the paper is unconvincing to the reviewer.—MERLE C. COULTER.

Heath and grassland.—FARROW[31] has described an interesting area of Norfolk and Suffolk Counties, England, where upon sandy soil with only 22.5 inches of annual rainfall there develops a transition from a heath dominated by *Calluna vulgaris* to a grassland with a short close turf in which *Festuca ovina* and *Agrostis vulgaris* are the most abundant species. The sterility of the soil is such that some has never been cultivated and much of the rest once farmed has long since been abandoned. The grassland seems to present the nearest approach to continental steppe conditions to be found in Great Britain.

In the second of his papers the author finds that the chief factor in the invasion of the heath by the grassland is the destruction of the *Calluna vulgaris* by an overpopulation of rabbits. Once the *Calluna* becomes weakened by its leaves being eaten by the rabbits, a luxuriant growth of *Cladonia* appears to be able to smother it and to hasten its death. In the absence of rabbits

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[29] Rev. in BOT. GAZ. **61**:82. 1916; **62**:160. 1916; **63**:419. 1917.

[30] RIDLEY, H. H., On endemism and the mutation theory. Ann. Botany **30**:551–574. 1916.

[31] FARROW, E. P., On the ecology of the vegetation of Breckland. I. General description of Breckland and its vegetation. Jour. Ecology **3**:211–228. 1915; II. Factors relating to the relative distribution of *Calluna* heath and grass heath in Breckland. Jour. Ecology **4**:57–64. 1916.

the *Calluna* maintains its dominance over both the grasses and the lichens.—GEO. D. FULLER.

The variable desert.—Writing in semipopular language, HARRIS[32] has described the wide variation of climatic and other factors influencing plant life in the desert region of Tucson, Arizona, in such a way as to give a more graphic and living picture of this most interesting region than will be found in other more voluminous and technical reports. The wide variation of precipitation from year to year and from month to month is made clear by a diagram, while the large proportion of waste of the scanty water supply is emphasized. The wide range of temperature during both the year and the day, the almost infinite variety of plant forms, extending from thin to thick-leaved herbs, from broad-leaved to leafless shrubs, and from succulent to woody plants with varied aspect at different seasons of the year, are all clearly depicted. In a word, the reader is made to appreciate some of the complexity of environment and diversity of organisms which have rendered this region so fascinating to the intelligent layman and to the investigating scientist.—GEO. D. FULLER.

Ecology of lichens.—In connection with a systematic study of the lichen flora of South Lancashire, WHELDON and TRAVIS[33] discuss some of the factors detrimental to the growth of these plants. Particular attention is directed to their sensitiveness to pollution of the atmosphere by the smoke and chemical fumes attendant upon the development of a manufacturing industry. The observations are of a general rather than of a particular character and are not accompanied by any experimental data. They also note that a calcareous substratum seems to counteract the effect of smoke upon the lichens. The selective action of these plants is well illustrated by the group of species peculiar to the carboniferous limestone.—GEO. D. FULLER.

Tolerance of trees.—After making studies of light in the forests of Michigan and Vermont and its effect upon the growth, BURNS[34] concludes that "tolerance" used to express a light relationship should no longer be used in reference to the development of tree seedlings. He found the filtered light in the forest of little value in the decomposition of carbon dioxide compared with the weakened white light. What is usually regarded as a light relationship is really the total relationship of a tree to all factors of the habitat. He further concludes that light readings in the forest are of little value.—GEO. D. FULLER.

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[32] HARRIS, J. ARTHUR, The variable desert. Scientific Monthly 3:41–49. 1916.

[33] WHELDON, J. A., and TRAVIS, W. G., The lichens of South Lancashire. Jour. Linn. Soc. 43:87–136. 1915.

[34] BURNS, G. P., Studies in tolerance of New England forest trees. III. Discontinuous light in forests. Vt. Agric. Exp. Sta. Bull. 193. pp. 23. 1916.

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NOTES ON BULBIFEROUS FUNGI WITH A KEY TO DESCRIBED SPECIES

J. W. HOTSON

(WITH PLATES XXI–XXIII AND SIX FIGURES)

Introduction

As has been shown in a former article (**6**), the term bulbil, as applied to fungi, refers to reproductive bodies of more or less definite form, composed of a compact mass of homogeneous or heterogeneous cells which may be few or many in number, but which are usually developed from primordia of more than one cell. This mode of reproduction is common among certain fungi and constitutes the only known means among others. Many of these structures superficially resemble the "spore-balls" of *Urocystis* or *Tuburcinia* among the smuts, but differ from them in their manner of germination. In general appearance and mode of development the bulbils of *Papulospora spinulosa* Hotson might readily be taken for "spore-balls" of *Urocystis*, but, on germination, promycelia bearing sporidia such as are produced by the smuts are not formed, nor is the production of these structures ever associated with the germination of bulbils. Other bulbils resemble compound spores of the *Stemphilium* type, but the latter are the result of successive divisions of single cells, while bulbils are derived from a group of initial cells to which new ones are added by a process of gemmation rather than formed by the septation of a single cell. Although this is true in general, in compound spores like those of

Stephanoma strigosum Wallr. the superficial cells are produced in a manner similar to those of certain bulbils. Mature bulbils may also resemble sclerotia. The latter, however, may be regarded as the result of the irregular massing together of vegetative filaments, the individual cells of which do not partake of the nature of spores either in appearance or structure, while in the bulbil those cells that are filled with protoplasm usually act independently of each other, in this respect resembling spores. There are a number of sclerotia of the simpler type, such as are produced by *Penicillium italicum* and its allies, which are small and more or less regular in form and outline, somewhat resembling bulbils in appearance. The mode of development of these sclerotia, however, consists in the irregular massing together of the vegetative filaments, as has just been mentioned.

Before 1912 the literature relating to bulbils dealt with less than a dozen described forms. Most of these were referred either to the form genus *Papulospora* or to *Helicosporangium*. Owing to the fact that the limitations of these two genera were not clearly defined, it was thought wise to redescribe the genus *Papulospora* (**6**), and to group all those fungi that produced bulbils, but whose perfect condition had not been obtained, into this form genus. The literature on this subject has been carefully reviewed in the article already mentioned. This article shows clearly that these fungi do not belong to any one of the natural orders, nor do they in any sense form a group by themselves, but occur without regularity as imperfect forms among the main groups of higher fungi. The forms, associated with bulbiferous conditions mentioned in that article, include among the Discomycetes a new species of *Cubonia*, among the Hypocreales 3 species of *Melanospora;* among the Basidiomycetes at least 4 types; while 9 species of *Papulospora* as yet unconnected with a perfect form are added to those already known. Among the latter, also, *Papulospora candida* Sacc. was found to be definitely connected with a second and well marked imperfect form, namely *Verticillium agaricinum* (Link) Corda var. *clavisedum* Sacc.

In 1914 NEGER (**9**) referred to a bulbiferous condition in connection with the life history of *Melanospora marchica* Lindau.

According to his account, the bulbils resemble the compound spores of *Urocystis* among the Ustilaginales. The color of these *Urocystis*-like spores is reddish to chocolate brown, their form more or less spherical, the cortex being a layer of empty, colorless cells. The size of the spore balls, however, is not given. They apparently resemble the bulbils of *Melanospora papillata* Hotson, but the perithecia of the two species are different. In *M. marchica* the perithecium has no papilla, the setae arising from the flush surface of the wall. The perithecium of *M. papillata*, on the other hand, has a distinct and often quite prominent papilla, the terminal setae being produced at its tip. The bulbils of *M. marchica* also resemble those of *Papulospora coprophila* (Zukal) Hotson, but vary somewhat in their mode of development. Apparently NEGER had not seen the writer's article dealing with bulbils (6) or that of BAINIER (1), and therefore makes no comparisons.

Recently DODGE (3, 4) has reported a species of *Papulospora* closely associated with *Ascobolus magnificus* Dodge. He is of the opinion that this is either a parasite on or an asexual spore form of the *Ascobolus*. These bulbils are light brown, with a layer of empty cells forming the margin. A description of this fungus is given in the present article under the name of *Papulospora magnifica*.

It has been shown in a recent article by MELHUS, ROSENBAUM, and SCHULTZ (8) that a species of *Papulospora* producing bulbils is frequently associated with the powdery scab of potatoes (*Spongospora subterranea* [Wallr.] Johnson). These investigators have isolated *P. coprophila* (Zukal) Hotson from tubers infected with powdery scab. This organism has been shown by inoculation experiments to be entirely saprophytic and in no way responsible for the disease. They believe, however, that the presence of bulbils of a species of *Papulospora* associated with *Spongospora* in the same sorus has probably been largely responsible for the confusion found in the writings of earlier investigators who observed numerous fungous threads in the sori, and in some instances spore balls that were quite different from those of *Spongospora*.

The cultural methods used in the study of the forms under consideration were similar to those described in a former paper (6).

The substrata were put in moist chambers, and as the bulbils appeared they were picked out with sterilized dissecting needles and transferred to tubes containing nutrient material.

Description of species

Bulbils are in all cases to be regarded as imperfect conditions of higher fungi. As has already been indicated, some have been definitely connected with perfect conditions belonging to widely separated genera of both Ascomycetes and Basidiomycetes. Those, however, that are to be considered in the present article have thus far baffled every effort to induce them to produce any perfect form, even after 7 or 8 years of cultural study. Two of these are doubtless Basidiomycetes, since their mycelia possess clamp connections, while another shows some evidence that it belongs to the Pyrenomycetes. It is the aim of the present article to contribute further information regarding the occurrence, morphology, and development of bulbils, and also to bring together the described species in the form of a key to the genus *Papulospora*.

Papulospora pallidula, n.sp. (figs. 1–16; text fig. 2).—Mycelium white, procumbent, scanty on most media; bulbils colorless, becoming pale yellow when old, somewhat spherical, 70–100 μ in diameter, sometimes elongated to 140 μ; primordium of two kinds, one a short lateral branch which divides dichotomously of 3 or 4 orders, occasionally more, and the other a group of intercalary cells. No other means of reproduction at present known.

On gross cultures of dog dung from Guatemala and Claremont, California; also on rabbit dung from Ontario.

The substrata were put into moist chambers and, when the bulbils appeared, transfers were made, eventually producing pure cultures. This fungus has been kept growing for more than 7 years on many different kinds of media, such as bran, prune, potato, cornmeal agar, etc. Thus far, however, all efforts to induce it to produce any other fructification than bulbils have failed. The bulbils are readily distinguished by their pale color. On a clear substratum they are almost colorless, while on horse dung or other dark media they become slightly yellowish or cream colored. As

is true with many other fungi, the abundance of the mycelium depends largely upon the kind of substratum. On potato or goat dung agar it develops very sparingly, often becoming quite difficult to detect even with a good lens, while on bran or cornmeal agar it becomes more conspicuous, growing evenly over the whole surface of the culture and on the sides of the tubes, but never becoming very flocculent. On appropriate media such as horse dung, bran, or cornmeal agar, the mycelium forms a thick felted layer over the substratum. Most of the hyphae are small, about 3–5 μ in diameter, but some of the older ones become as large as 10 μ, with prominent cross walls. They are frequently packed with large oil globules (fig. 1). Here and there in the hyphae swollen cells appear that are full of food material. These are oval at first, but eventually become almost spherical.

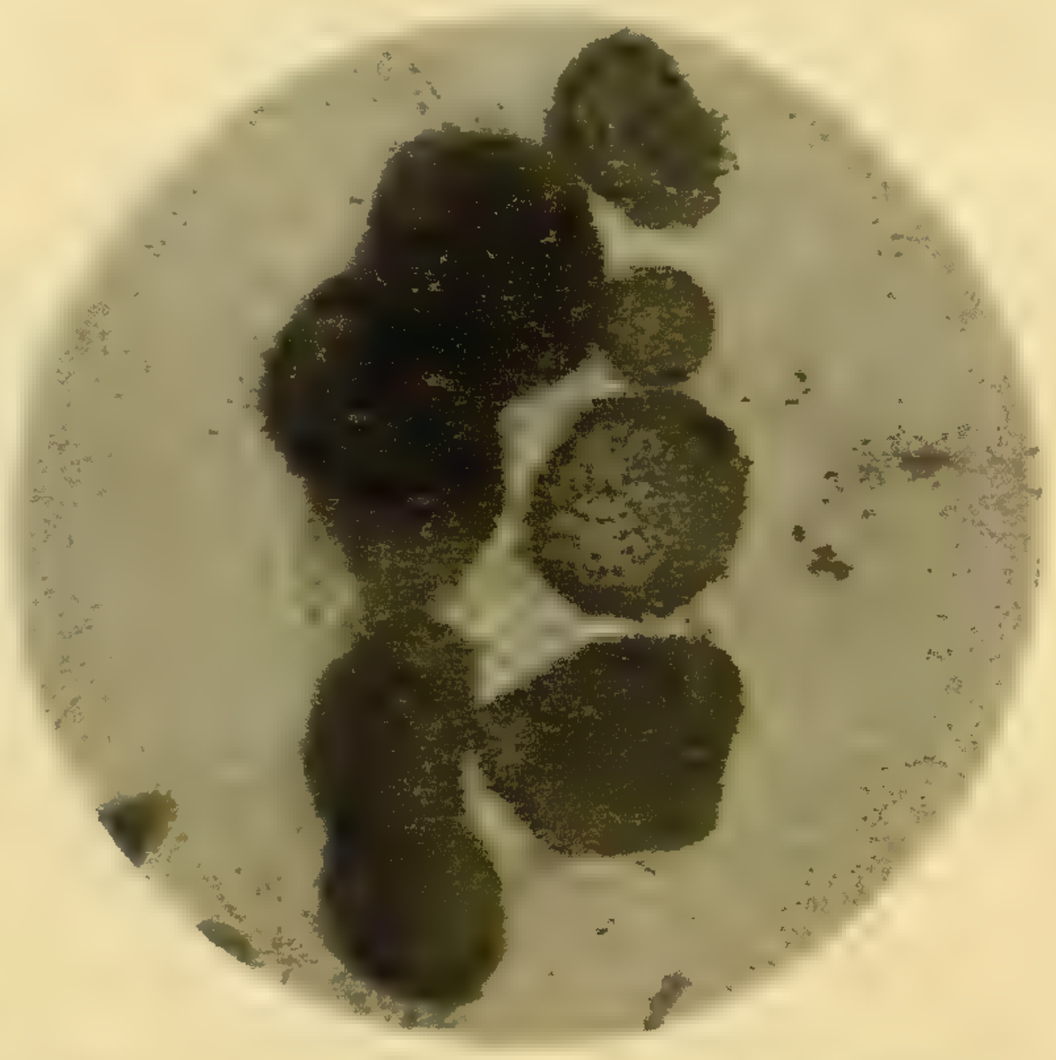


FIG. 1.—Group of bulbils of *P. byssina*, showing variations in size.

DEVELOPMENT OF BULBIL.—A short lateral branch divides dichotomously, producing dichotomies of the second, third, or sometimes of the fourth order (figs. 2–6). These branches divide into short cells which enlarge, eventually forming the central ones of the bulbil. As these cells grow they become more compact, and from them by a process of budding others are formed which increase in size, becoming closely and compactly pressed against their neighbors (figs. 7–9). This mode of development usually produces mature bulbils that are more or less spherical in form and measure 70–100 μ in diameter (fig. 13).

A second mode of development of the bulbil is sometimes observed. Intercalary cells become swollen, having absorbed a large quantity of food material. From these large cells others are produced by a process of gemmation, and these in turn bud off others and so on (figs. 10–12). Eventually a bulbil that is very

pale in color is formed, with several large cells in the center which are conspicuously filled with oil globules. These bulbils are usually more or less spherical, but not infrequently become elongated, as shown in text fig. 2, which shows a group of bulbils, the longest of which measures 78 by 140 μ and is probably the result of the fusing of two immature forms. These bulbils germinate readily in water. Fig. 13 shows a germinating bulbil 75 by 67.5 μ in diameter after 24 hours in a Van Tieghem cell. The young hyphae, which have a large number of oil globules, are usually produced from the larger cells, but any cell is capable of germination. Occasionally as the bulbils grow older the cells composing them adhere less firmly together, becoming more and more like independent spores (fig. 14). It requires only a slight pressure to force them apart. This resembles the condition found in connection with the development of the bulbil of *Papulospora polyspora* Hotson (6), which in turn suggests a similar condition found in *Aegerita webberi* Fawcett (5). Fig. 14 shows a few of these loosely connected cells germinating, which seem to act independently, like spores.

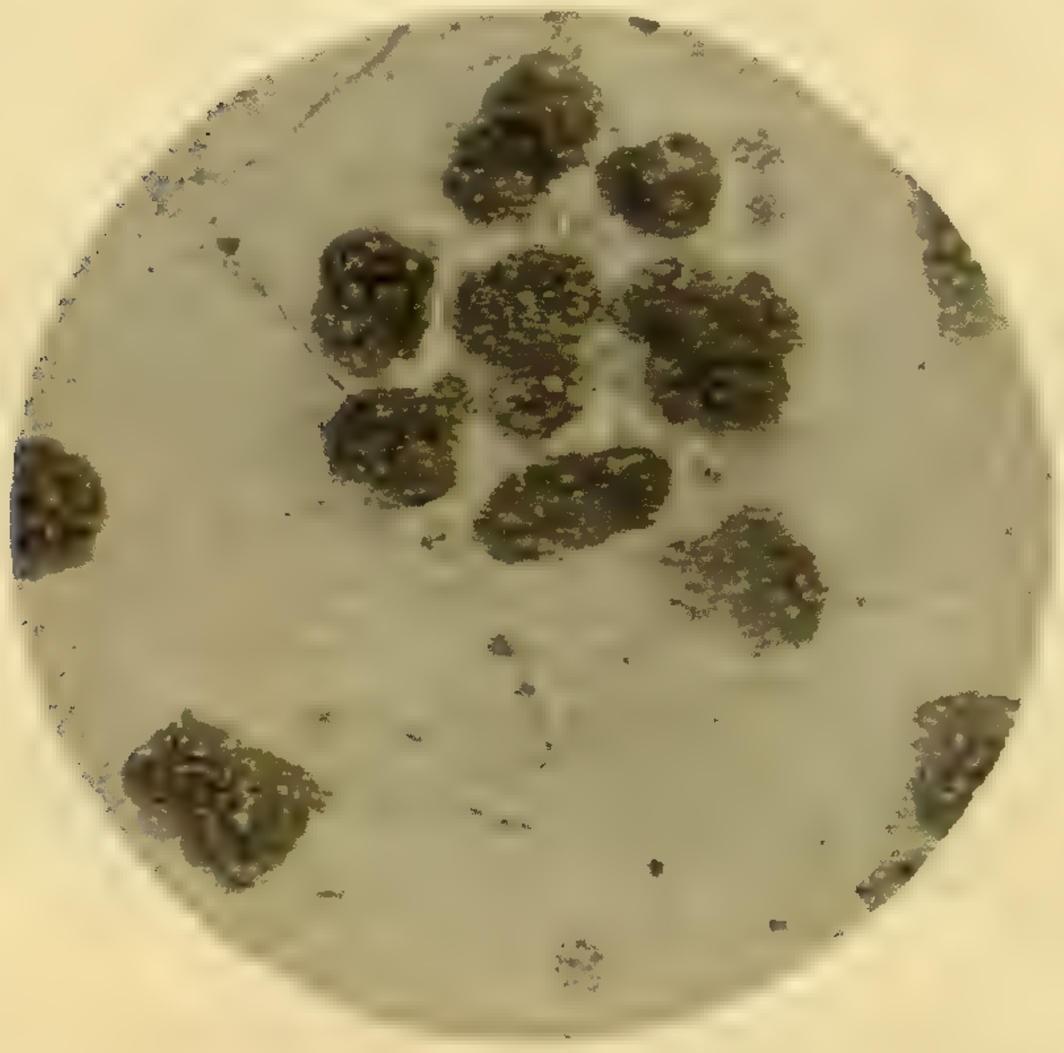


FIG. 2.—Group of bulbils of *P. pallidula*.

It is probable that one of the primordia just described is that of the perfect stage, but for some reason it fails to develop further. This view is strengthened by the fact that on several occasions perithecium-like structures over a millimeter in diameter have been found, as if an effort were being made by the fungus to produce the perfect stage. Thus far, however, none of these have been induced to develop sufficiently to produce spores.

Papulospora byssina, n.sp. (figs. 17–24; text fig. 1).—Mycelium white, procumbent, scanty on most media; bulbils light straw or cream colored, becoming brownish with age, more or less spherical

in form, 100–250 μ, occasionally elongated to 350 μ in diameter, produced in fluffy aerial clusters; primordium one or more short lateral branches twining spirally about the main branch. No other means of reproduction at present known.

On horse dung, Kittery, Maine; Seattle, Washington; St. Louis, Missouri.

The original material from which pure cultures of this fungus were obtained was found on a horse dung compost at Kittery, Maine, by Dr. THAXTER. It has since been found by the writer on similar material in the vicinity of Seattle; also on material sent from St. Louis, Missouri, by S. M. ZELLER. In the last instance the bulbils apparently were produced after the horse dung compost had been used as a fertilizer on mushroom beds. This fungus has never been found on any other substratum than horse dung. It has been grown on different media in pure cultures for 6 years without inducing it to produce any other fructification than bulbils.

The mycelium is white, 3–5 μ in diameter. It is usually procumbent, but when cultures are left in such a position that the hyphae can grow straight downward they grow out into the air, producing long streamers or festoons which attach themselves to the opposite side of the test tube.

The bulbils of *P. byssina* resemble those of *Grandinia crustosa*, but the two species can easily be distinguished by the prominent clamp connections in the mycelium of the latter. Even the general appearance of the mycelium in cultures is sufficient to distinguish them, *Grandinia* producing characteristic "white, fibrous, ropelike strands of hyphae which radiate conspicuously in all directions from the point of inoculation." This phenomenon is entirely absent in *P. byssina*. The cells composing the bulbils are homogeneous throughout. In this respect they resemble those of *P. sporotricoides* and *P. cinerea*, but in the former species the bulbils are small, 20–36 μ in diameter, and chocolate brown, while in the latter they are about the same size but steel gray. In *P. byssina*, however, the bulbils are large, 100–250 μ in diameter, and straw color.

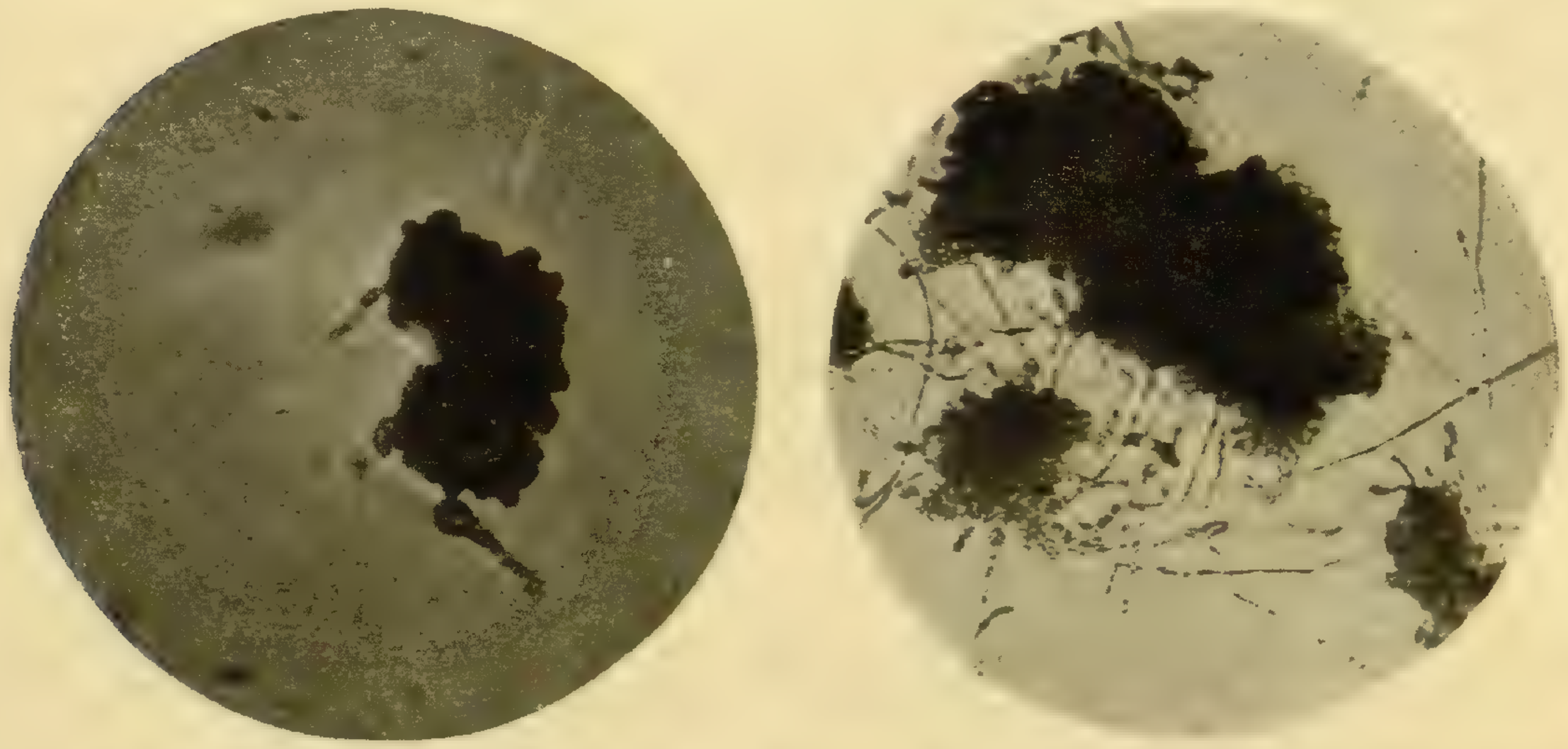
DEVELOPMENT OF BULBIL.—In most cases the primordium of the bulbil consists of a short lateral branch which may or may not divide dichotomously. This branch coils around the main hypha

(fig. 17), which may send out other lateral branches near the first (fig. 19). This branch may also take part in the formation of the bulbil. The cells of these various branches increase in size and become well supplied with food material. From them short lateral branches are produced which either intertwine among each other, or if very short assume the form of new cells as if produced by a process of budding or gemmation. Fig. 20 shows the primordium of a bulbil in which the secondary branches are being produced. These will eventually intertwine with each other in a more or less wormlike fashion, as shown in fig. 21, an immature bulbil 44 μ in diameter. The first lateral branches that twine around the primary filament may become localized, in which case the mature bulbils will be somewhat spherical, as shown in fig. 22, which represents a bulbil 110 μ in diameter. More often, however, the spherical bulbils are produced in a slightly different way. Not infrequently a terminal branch coils up and winds back on itself, or it may divide dichotomously, both branches thus formed twining back on the main filament (fig. 18). A primordium of this sort develops in the same way as the one already described, by the intertwining of lateral branches. The mature bulbil, however, tends to be more spherical than that in which a lateral branch twines about the primary filament. Occasionally several bulbils may be produced from the same filaments, as is indicated in fig. 24, which shows the beginnings of 3 bulbils at *a*, *b*, and *c* respectively. At *a* the secondary branches are beginning to be formed in a manner similar to that shown in fig. 20. It is possible that *a* and *b* will merge into one, forming an elongated and more or less irregular bulbil (text fig. 1). Owing to the variation in the mode of development, a great diversity of form is produced. Text fig. 1 represents a group of bulbils showing this wide variation of form. The exact dimensions of these bulbils vary from 112.5 to 338 μ, but occasionally even a greater difference than this is observed.

To test the germinating power of these fruiting bodies, hanging drops were made in Van Tieghem cells. It was found that in 24 hours many of them had begun to germinate, and in 48 hours numerous hyphae were developed. Fig. 23 represents a portion of a germinating bulbil after 48 hours.

Papulospora aurantiaca, n.sp. (figs. 25–38; text figs. 3, 4).—Mycelium white at first, becoming yellowish with age, procumbent, scanty on most media, densely filled with oil globules, clamp connections sparingly produced; bulbils pale yellow, becoming orange, nearly spherical, frequently aggregated, 100–250 μ in diameter; primordium a spiral of one or two turns. No other mode of reproduction at present known.

On bark collected by Dr. THAXTER near Port of Spain, Trinidad, W.I.



FIGS. 3, 4.—*P. aurantiaca:* fig. 3, mature bulbil; fig. 4, several germinating bulbils.

The mycelium of *Papulospora aurantiaca* is somewhat inconspicuous, the hyphae being small, usually about 2.5–3.5 μ in diameter, and scanty. On certain media, like cornmeal or bran agar, it becomes more marked but never profuse on any media tried. These included such nutrient material as potato, sugar, bran, cornmeal, prune juice, horse dung, various kind of wood, etc. The hyphae contain large numbers of oil globules which vary considerably in size. When the filaments are crushed these float out into the water, a number frequently fusing together and sometimes forming large spherical globules 17.5 μ or more in diameter.

Many and varied experiments have been made in the hope of causing the fungus to produce its perfect form, but thus far all efforts have failed. That it is a Basidiomycete is readily seen by the presence of clamp connections in the mycelium. These are

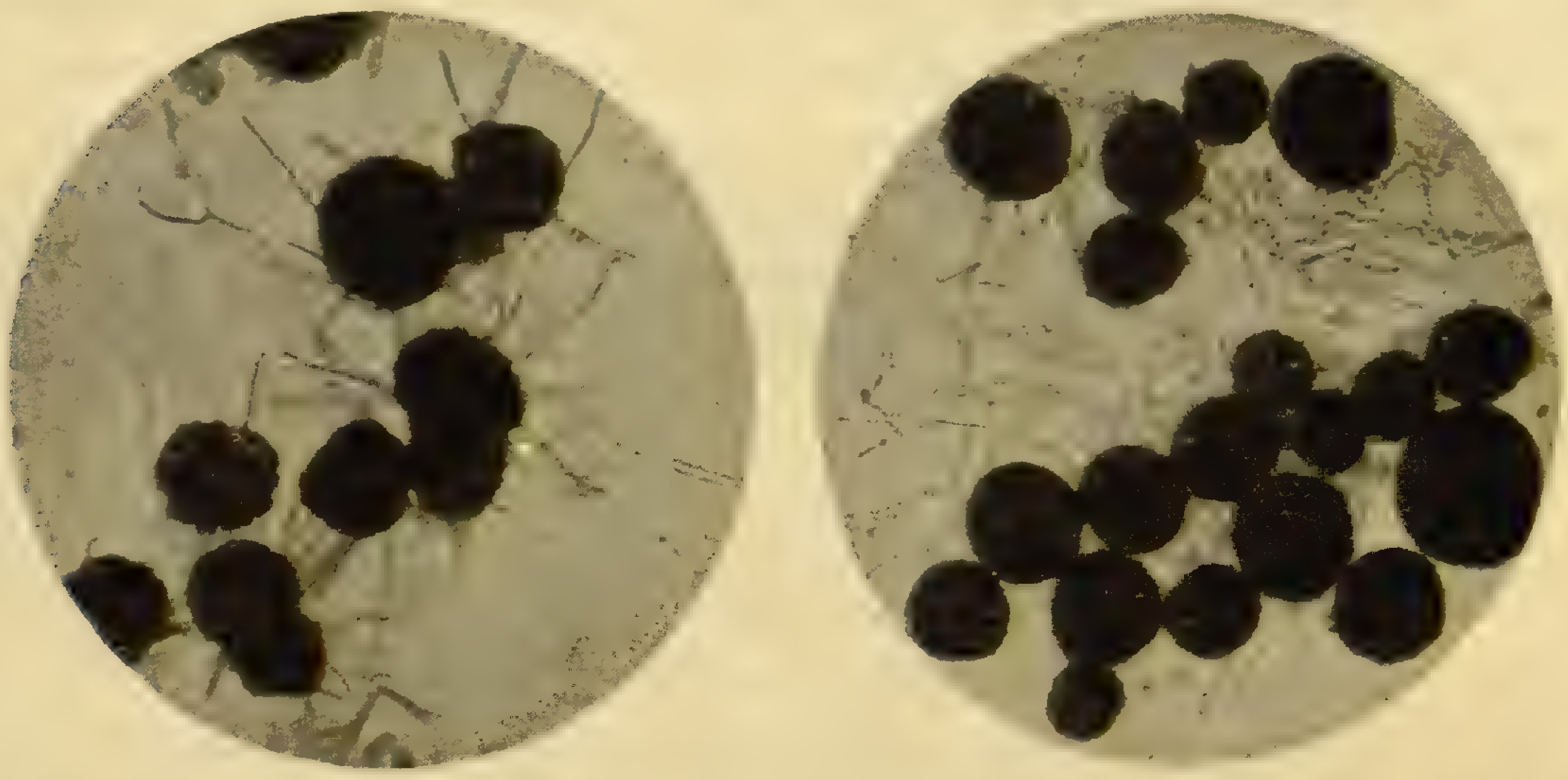
small, more or less inconspicuous, and sparingly developed. There are a number of basidiomycetous forms that produce bulbils as an imperfect condition. In a former contribution (6) the writer has referred to 4 such species, and in the present article 2 additional ones are described. The reddish orange color of the bulbil under consideration readily distinguished it from other species having clamp connections. The bulbils of *P. nigra* and *P. anomala* are dark brown or black, those of *Corticium alutaceum* chocolate brown, and those of *Grandinia crustosa* straw colored with conspicuous clamps.

Samples of the fruiting bodies of *Sporodesmium aurantiacum* B. and C., collected by Dr. THAXTER at Cranberry, North Carolina, in August 1889, were obtained from him for comparison with the bulbils of *P. aurantiaca*. As these structures were too old to germinate, a comparison of their mode of development could not be made. The fruiting bodies of the two fungi resemble each other so closely in their general form, color, texture, etc., however, that there is little doubt but that they are identical.

DEVELOPMENT OF BULBIL.—In common with many other bulbils, those of *P. aurantiaca* begin by a short lateral branch coiling up spirally. The early stages in the development, with some of the variations, are illustrated in figs. 25–38. During the process of coiling, which seldom results in more than two turns, the individual cells comprising the primordium become well supplied with food material and often appear distended (figs. 26, 27, 29). From the cells composing the coil short branches are developed (figs. 27, 28, 31, 32). These secondary branches may twine about each other or they may enlarge, forming cells that resemble those produced by a process of gemmation in other bulbils. These short branches and cells continue to be formed, sometimes on the concave side of the curve, sometimes on the convex side, until eventually all trace of the original coil has disappeared and the bulbil takes on the appearance of a homogeneous mass of cells, more or less irregular in shape, but on the whole somewhat spherical. Not infrequently around the margin of the developing bulbil numerous free twining ends of short branches are seen in loops and coils that are more or less characteristic (figs. 37, 38). This condition is also seen in

the fruiting bodies of *Sporodesmium aurantiacum* B. and C., already mentioned. In their early development the bulbils are usually very irregular in outline, owing to the projection of secondary branches which become less prominent in the mature form.

Frequently the bulbils appear as orange or yellowish patches scattered over the surface of the culture instead of being distributed evenly. This is due to the fact that the primordia are often produced in large numbers on a single branch, as shown in figs. 35, 36. As these develop, a corresponding number of bulbils are produced, which adhere together for a considerable time, superficially



FIGS. 5, 6.—*P. nigra:* fig. 5, group of germinating bulbils; fig. 6, group of mature bulbils, showing general form and variations in size.

resembling sclerotia. As a rule, these bulbils develop very slowly, usually taking several months before they mature. Eventually, however, as the substratum becomes dried up, the individuals separate into powdery, orange colored masses. The bulbils germinate readily in nutrient fluid, several of which are shown in text fig. 4.

Papulospora nigra, n.sp. (figs. 40–47; text figs. 5, 6).—Mycelium white, procumbent, scanty, oil globules and clamp connections conspicuous; bulbils colorless at first, becoming dark brown to black, nearly spherical, 100–180 μ in diameter at maturity; primordium one or more short lateral branches which coil up and intertwine. No other means of reproduction at present known.

On old cardboard, Cambridge, Massachusetts, and on hardwood chips, Seattle, Washington.

Papulospora nigra was obtained from gross cultures of old cardboard in the cryptogamic laboratories of Harvard University, and on similar cultures of chips in the botanical laboratory of the University of Washington, Seattle. When the bulbils appeared, pure cultures were made in a manner similar to that already described. This species has been grown on a variety of media for 8 years without the perfect condition being obtained. The mycelium is white and remains so throughout the period of rapid growth. Only when the hyphae get old do they begin to change color, becoming brownish or smoke colored. The primary mycelium is procumbent and on most media is inconspicuous, but becomes more or less flocculent or cobwebby on bran or prune agar. When a culture becomes old, the whole surface is covered with black bulbils which completely obliterate the mycelium. The hyphae frequently contain many large, conspicuous oil globules (figs. 40–42). The mycelium also has quite prominent clamp connections, a condition indicating its relation to the Basidiomycetes.

The bulbils of this species resemble closely those of *P. anomala* Hotson (6) in size, form, and color. They are readily distinguished, however, by their mode of development. In the latter species the bulbils arise from "slightly swollen, colorless, intercalary cells . . . . about 4 or 5 μ in diameter, sometimes projecting considerably and resembling short stunted branches; at other times the base of a short lateral hypha swells slightly and forms the primordium." From these primordial cells branches are sent out in different directions, the lateral walls of the basal cells adhering firmly together and becoming eventually incorporated into the bulbils. It will be seen that the development of the bulbil of *P. nigra* is quite different from this. It has already been shown in the consideration of *P. aurantiaca* that the bulbils of *P. nigra* may readily be distinguished from those of *Corticium alutaceum*, and also from those of *Grandinia crustosa* by their color.

DEVELOPMENT OF BULBIL.—From the primary hyphae short lateral branches, which coil up spirally, arise, producing one or two turns (figs. 42, 43). From the cells of these spirals short branches

are developed which intertwine, sometimes incorporating the primary filament. If the lateral branch divides, as it not infrequently does, the two filaments thus formed coil up, and these with those that are subsequently produced from them intertwine (figs. 44, 45). During the early stages of development the cell walls are usually clearly distinguished, but as the bulbil grows they become more or less transparent and quite indistinct (figs. 45, 46). At the stage represented in fig. 46 the whole bulbil is colorless, the cells containing a large number of oil globules, which condition continues until almost maturity, when they begin to turn brownish. The walls gradually become more pronounced, and on account of lateral pressure they assume a more definitely angular condition. As the bulbils increase in size they become more and more spherical, so that at maturity they have a clear cut, even margin. Text fig. 6 represents a group of these bulbils. Although they vary considerably in size, the general spherical form and even outline is maintained throughout. Sometimes elongated, irregular bulbils are formed when two primordia happen to be close together and fuse as they develop. These, however, are the exceptions, and the cause of their abnormal condition can usually be detected. If the bulbils are produced rather sparingly or away from each other, they invariably become spherical.

These bulbils germinate readily in sterile water in a Van Tieghem cell or in a watch glass. Fig. 47 illustrates the germination of a bulbil, 100 μ in diameter, after 48 hours in a hanging drop. Text fig. 5 represents germinating bulbils after 3 days. It may be noticed that they are not so even in outline as in text fig. 6. The probable reason for this is that, as the hyphae are produced, the marginal cells become forced aside and disarranged, particularly when the germinating tubes come from other than cortical cells.

Papulospora magnifica, n.sp. (figs. 39, 48–69).—Mycelium white, procumbent, scanty; bulbils light brown, becoming darker with age, spherical, 37–50 μ in diameter, with one, occasionally two large central cells surrounded by a single row of cortical ones which become empty at maturity; the primordium a short lateral branch of which the terminal and occasionally also penultimate cell enlarge.

On horse dung in moist chamber cultures, New York City.

In June 1915 the writer obtained a pure culture of *Papulospora magnifica* from Dr. B. O. DODGE for identification, with permission to make a cultural study of it. The fungus was originally found in New York City in April 1912, associated with *Ascobolus magnificus* Dodge, growing on horse dung in moist chamber cultures. DODGE (3) is inclined to consider this as parasitic on the mycelium of *A. magnificus*, having traced "a direct connection between the mycelium of the parasite . . . . and the mycelium of the host." He also shows by figures this definite connection. In a later statement (4) he suggests that the *Papulospora* may be associated with *Ascobolus magnificus* "either as a parasite or as an asexual spore form of the *Ascobolus*. If the former is the case, the mycelium of the parasite is intrahyphal; if the latter is true, then the phenomenon known as 'Durchwachsung' is extremely complicated in the mycelium of this *Ascobolus*."

As has already been indicated, bulbils must in all instances be regarded as representing imperfect conditions of the higher fungi; and, like the members of other more or less clearly defined form genera, may be associated with perfect conditions included in wholly unrelated genera of the Ascomycetes and Basidiomycetes. A bulbiferous condition has been found associated with the genus *Cubonia* (6) belonging to the same family as *Ascobolus*, so that it is not inconsistent with the general characteristics of the form genus *Papulospora* to consider the bulbils of *P. magnifica* as an imperfect condition of *Ascobolus magnificus*. All efforts, however, have failed to obtain the ascocarp from pure cultures of the bulbils, although repeated attempts have been made to do so by growing the fungus on a great variety of media which were exposed to different constant temperatures. Although the majority of the species of *Papulospora* are undoubtedly saprophytic, there are some reported as parasitic. *P. parasitica* (Karsten) Hotson was described by KARSTEN (7) as parasitic on beets, while COSTANTIN (2) described *P. dahliae* as connected with the roots of dahlias, but does not state definitely that it is parasitic, although that is the general impression one obtains from his article.

In the light of the general characteristics of the genus *Papulospora* and the fact that the hyphae of *P. magnifica* have been

definitely traced for some distance inside the filaments of *Ascobolus magnificus*, we are led to the conclusion that the fungus under consideration is parasitic on the latter rather than that the bulbil is the imperfect condition of it. On all the cultures made of *P. magnifica* the mycelium grew very sparingly, being procumbent, and at times growing down into the medium, but never becoming flocculent or aerial. On potato, bran, prune, and cornmeal agar only a small amount of mycelium was produced even after several months. So meager was the development that it might easily have been overlooked unless examined carefully with a hand lens. Of the different media tried, a decoction of horse dung with agar or the horse dung itself, sterilized in an Arnold's steam sterilizer, proved the most satisfactory.

A microscopic examination frequently showed the mycelium to be a network of anastomosing hyphae (fig. 69), while at other times (figs. 65–68) enlarged food storage cells were found, the largest being 15 μ in diameter.

DEVELOPMENT OF BULBIL.—The primordium of the bulbil is quite easily recognized as a short lateral branch, somewhat coiled or curved and well filled with granular material. In this development the bulbil seldom, if ever, produces a coil crosier fashion, such as does *P. parasitica*, which it most closely resembles. From the end of this coiled branch a cell is cut off, enlarges, and becomes well filled with granular food material (figs. 54, 55). This cell eventually develops into the large central cell of the bulbil. Occasionally this lateral branch twists on itself, as represented in figs. 51, 53, while at other times a secondary branch is formed from it (figs. 50, 52). The usual mode of procedure, however, is that shown in figs. 48, 49, 54, 55. It may be seen that the end cell continues to enlarge, subsequently becoming almost spherical, reaching a diameter of 10–20 μ. Before it reaches its mature size, however, several short branches, which grow over the surface, are given off from it (figs. 55–59). These branches intertwine, clinging close to the wall of the enlarged cell, finally inclosing it, so that the mature bulbil consists of a single large central cell, rich in food material, surrounded by a layer of cortical cells produced by these branches becoming compacted firmly together

laterally. In the course of development these outer cells lose their protoplasmic contents, although the walls retain more or less of the brownish color.

Although the foregoing description of the mode of development of the bulbil is the usual one, not infrequently a second large cell is formed by the primordial branch (figs. 62, 63). In such instances the further development is practically the same as where there is a single central cell. The lateral branches which eventually become the cortex are produced from both the large cells, which subsequently become completely surrounded, precisely as in the case already described.

Germination of bulbil

The bulbils of most of the species of *Papulospora* germinate with little difficulty. All of those described in this article, with the exception of *P. magnifica*, have been found to produce germ tubes quite readily. In the study of that species various media were employed in the hope that a favorable condition might be found for the germination of the bulbils. Among these were bran, potato, and prune agar, various synthetic media, as well as decoctions of horse dung used both as a liquid and associated with agar, but all these failed to produce the desired result. Finally a method that the writer had found successful in inducing the ascospores of certain species of *Ascobolus* and *Cubonia* (**6**) to germinate was tried with some success. Mature bulbils were put on a flamed glass slide and carefully crushed with the flat surface of a scalpel. They were then transferred to hanging drops of nutrient media, a sterile decoction of horse dung proving the best. Many of the bulbils thus crushed were totally destroyed, but in a few instances, where the pressure was just sufficient to break the cortical layer of cells without injuring the large central one, germination was produced and a branching filament soon developed (fig. 39).

The mature bulbil of *P. magnifica*, with one or two large central cells surrounded by empty cortical ones, superficially resembles certain bulbils of *P. coprophila* (Zukal) Hotson. The latter, however, consists of 1–4 (sometimes as many as 10) large central cells, only occasionally having a single central cell. Moreover, the

spiral primordium of *P. coprophila* and the flocculent and abundant mycelium differ widely from those of *P. magnifica*. The bulbils of *P. magnifica* more closely resemble those of *P. parasitica* (Karsten) Hotson than they do those of *P. coprophila*. However, in *P. parasitica*, which is described as parasitic on beets in the original description by KARSTEN, the mycelium is flocculent, the bulbils 15–21 μ in diameter, with a single large central cell invariably present, and the primordium a spiral which coils crosier fashion. Thus, the procumbent and scanty character of the mycelium of *P. magnifica*, as well as the size and mode of development of the bulbil, readily distinguish it from *P. parasitica*. In order to obtain further information regarding the relationship of these two fungi, inoculations were made in the roots of growing beets and turnips, both in the field and in the laboratory. In each case a small slice of the root was removed with a sterile knife and a cavity made in the cut surface. From a pure culture of *P. magnifica* a portion of the nutrient agar containing bulbils and mycelium was gouged out and deposited in this cavity. Over this a small piece of glass was put and the soil replaced. Although several similar experiments were carried on, no indication of a parasitic condition could be detected.

Other species that resemble the two just mentioned, such as *Physomyces heterosporus* (*Monascus heterosporus* [Harx] Schröter), *Dendryphium bulbilferum* Zukal, *Acrospeira mirabilis* Berk. and Br., etc., have already been discussed (**6**), so that it is not necessary to repeat the discussion.

Key to species of bulbiferous fungi

There are several more or less well defined characteristics that are made use of in making the following key for the members of the form genus *Papulospora*. A broad division is readily made on the presence or absence of clamp connections in the mycelium. Those forms which do not have this condition are grouped into 4 categories based on the color and size of the bulbil, namely, colorless to cream, steel gray, black, and yellowish red to dark brown. Another character used, especially in the last mentioned division, is the mode of development of the bulbils, whether from intercalary

cells, a single lateral branch, or a group of vertical hyphae. Using these characters as a fundamental basis for separation, the described species of bulbiferous fungi may be distinguished as follows:

Hyphae with clamp connections
Bulbils dark brown to black
Bulbils 65–80 μ in diameter, chocolate brown ..... *Corticium alutaceum*
Bulbils 125–175 μ in diameter, dark brown or black; margin even
Primordium intercalary ..... *Papulospora anomala*
Primordium spiral ..... *Papulospora nigra*
Bulbils light yellow, 52–88 μ in diameter; hyphae conspicuous, ropelike *Grandinia crustosa*
Bulbils yellow, becoming orange, 100–250 μ in diameter; hyphae formed evenly ..... *Papulospora aurantiaca*
Hyphae without clamp connections
Bulbils colorless, pale yellow, or cream colored
Bulbils cream colored, 30–35 μ in diameter; parasitic on *Geoglossum* *Papulospora candida*
Bulbils colorless or pale yellow, 70–100 μ in diameter, saprophytic *Papulospora pallidula*
Bulbils steel gray, 21–36 μ in diameter ..... *Papulospora cinerea*
Bulbils black or smoke color
Bulbils 75–100 μ in diameter; margin even ..... *Cubonia bulbifera*
Bulbils 200–300 μ in diameter; margin irregular .... *Papulospora pannosa*
Bulbils yellowish red to dark brown
Bulbils scanty; perithecia usually present
Perithecia with neck and lateral and terminal setae *Melanospora cervicula*
Perithecia with papilla and terminal setae ..... *Melanospora papillata*
Bulbils abundant; perithecia usually absent
Primordium intercalary
Bulbils brownish yellow; central cells 28–55 μ in diameter *Papulospora immersa*
Bulbils straw color; central cells 10–20 μ in diameter *Papulospora irregularis*
Primordium one or more lateral branches
Primordium normally a single lateral branch
Primordium spiral
Cells of the bulbil heterogeneous; cortex definite
Normally only one central cell
Cortex complete
Mycelium scanty, procumbent; bulbil 37–50 μ in diameter; occasionally two central cells *Papulospora magnifica*

Mycelium abundant, flocculent; bulbil 15–21 μ in diameter; invariably 1-celled . . . *Papulospora parasitica*

Cortex incomplete . . . . . *Acrospeira mirabilis*

Normally more than one central cell

Spiral in one plane; cortical cells spinulose *Papulospora spinulosa*

Spiral normally in more than one plane; not spinulose; 2–6 central cells

Bulbils dark brown . . . . . *Papulospora coprophila*

Bulbils brick red . . . . . *Papulospora rubida*

Cells of bulbil homogeneous throughout

Bulbils chocolate brown, 21–36 μ in diameter, producing *Sporotrichum* spores . . . . . *Papulospora sporotrichoides*

Bulbils straw color, 100–250 μ . . . . . *Papulospora byssina*

Primordium not spiral; bulbils large, irregular, 100–750 μ in diameter . . . . . *Papulospora aspergilliformis*

Primordium two or more lateral branches forming a spherical aggregation of cells at the top . . . . . *Papulospora polyspora*

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EXPLANATION OF PLATES XXI–XXIII

The drawings for the plates were made with the aid of a camera lucida, using different combinations of the Bausch & Lomb lenses. All the stages

in the development of bulbils were drawn with the same magnification, using 4 mm. objective and no. 12 eyepiece. The text figures are microphotographs taken by W. J. WESTERBERG. The plates have all been reduced in reproduction about three-fourths.

FIGS. 1–16.—*Papulospora pallidula.*

FIG. 1.—Hypha showing large oil globules.

FIGS. 2–6.—Dichotomously dividing primordium.

FIGS. 7, 8.—Primordia more or less irregular in their dichotomous branching.

FIG. 9.—Further development of bulbil.

FIGS. 10–12.—Second mode of forming a bulbil.

FIG. 13.—Mature bulbil germinating.

FIG. 14.—Cells of an old bulbil loosely adhering to each other; some of cells germinating.

FIGS. 15, 16.—Terminal primordia.

FIGS. 17–24.—*Papulospora byssina.*

FIGS. 17–19.—Different forms primordium may assume.

FIGS. 20–22.—Stages in development of bulbil.

FIG. 23.—Germinating bulbil.

FIG. 24.—Primordia of at least 3 bulbils from same filament at *a*, *b*, and *c* respectively.

FIGS. 25–38.—*Papulospora aurantiaca.*

FIGS. 25–32.—Variations in mode of coiling of primordium of bulbil.

FIGS. 33–38.—Other states in development of bulbil.

FIG. 39.—Germinating bulbil of *Papulospora magnificus.*

FIGS. 40–47.—*Papulospora nigra.*

FIG. 40.—Portion of hypha showing large oil globules and clamp connection.

FIG. 41.—Form of primordium that sometimes occurs.

FIGS. 42–46.—Successive stages in development of bulbil.

FIG. 47.—Mature bulbil germinating.

FIGS. 48–69.—*Papulospora magnifica.*

FIGS. 48, 54–60.—Stages in development of bulbil.

FIGS. 49–53.—Forms of primordium that occasionally appear.

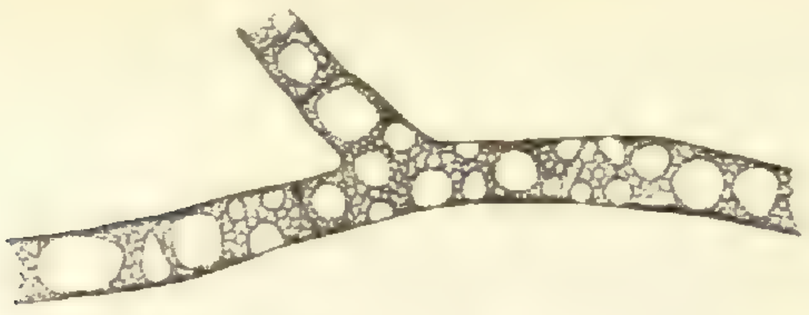
FIG. 61.—Median section of mature bulbil.

FIGS. 62, 63.—Stages in development of bulbil with 2 large central cells.

FIG. 64.—Median section of mature bulbil with 2 large central cells.

FIGS. 65–68.—Portions of hyphae with large storage cells densely filled with food material.

FIG. 69.—Portion of normal mycelium showing tendency to anastomose.



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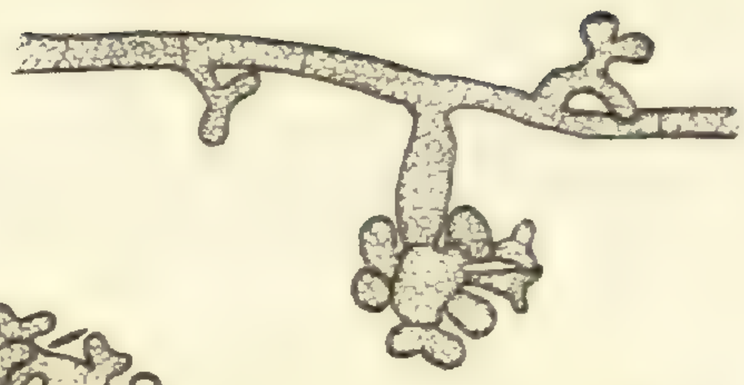

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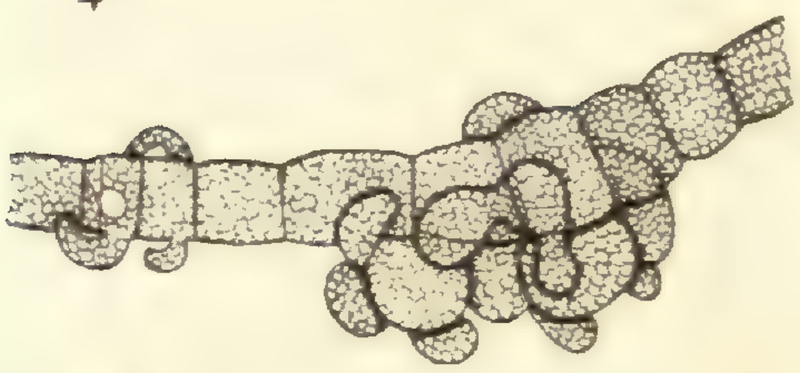

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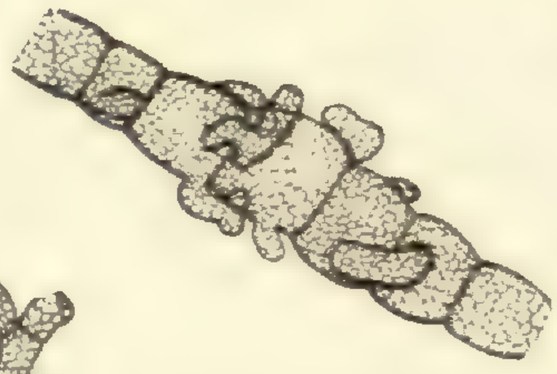

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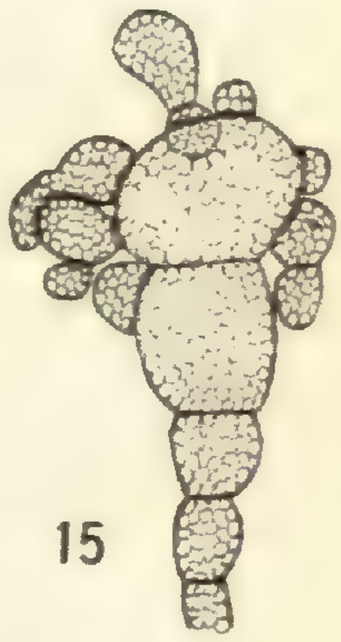

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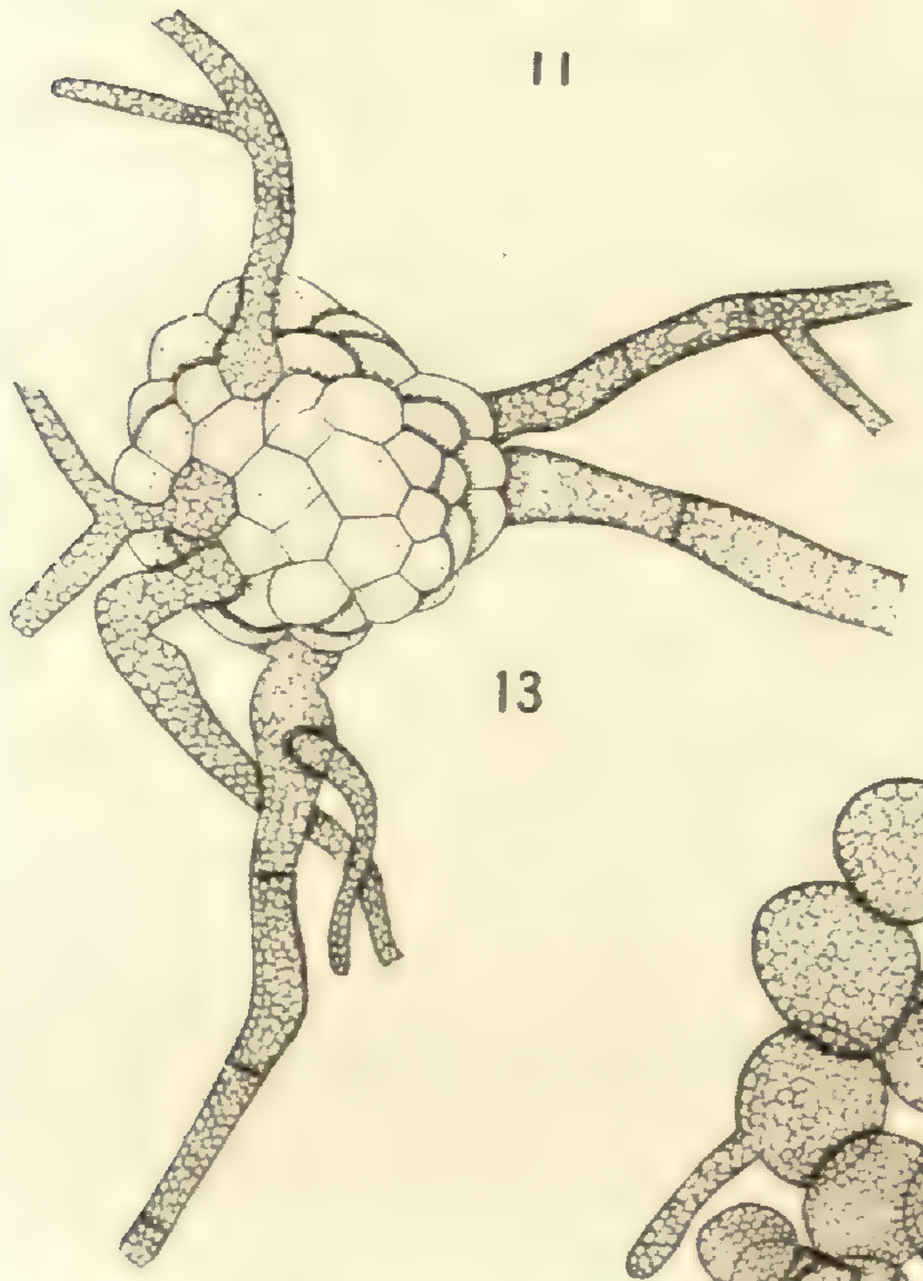

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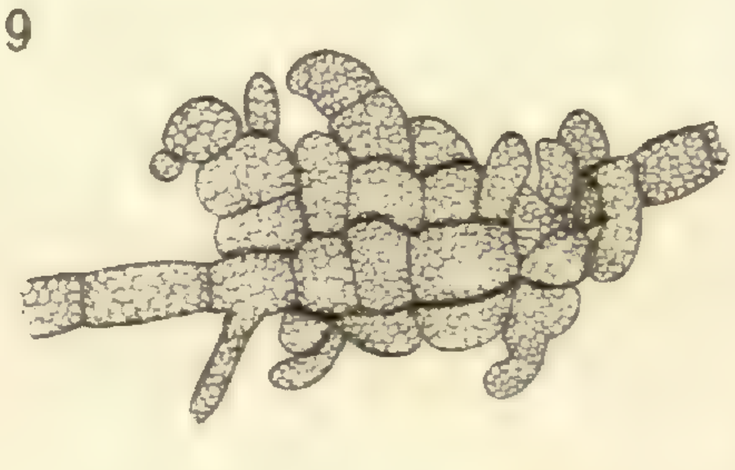

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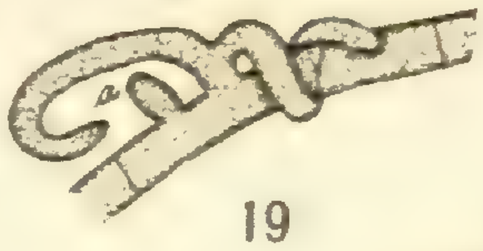

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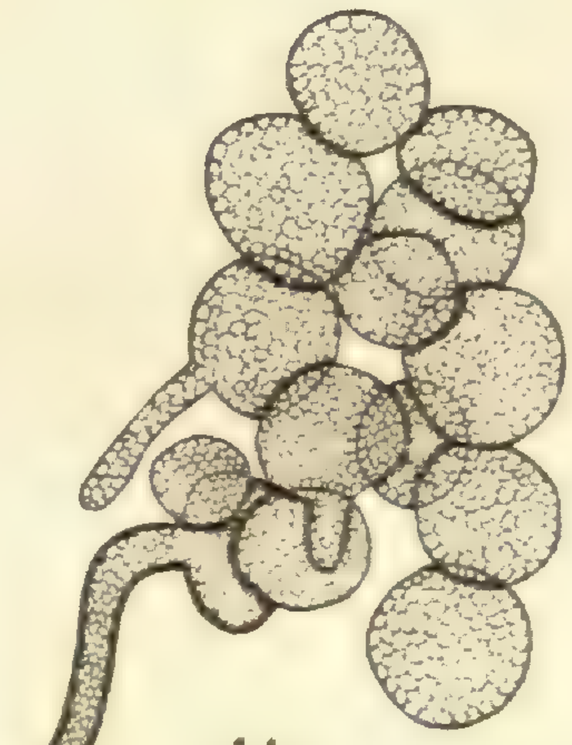

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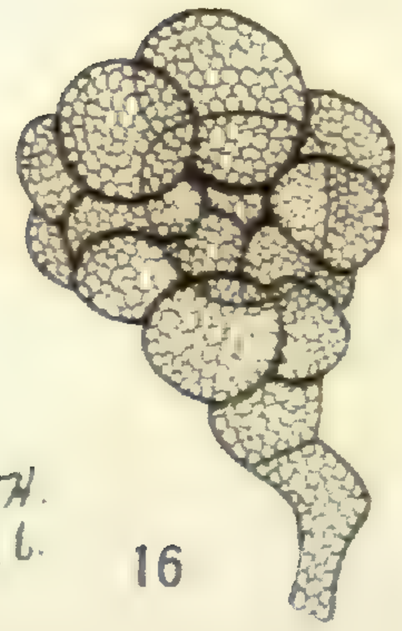

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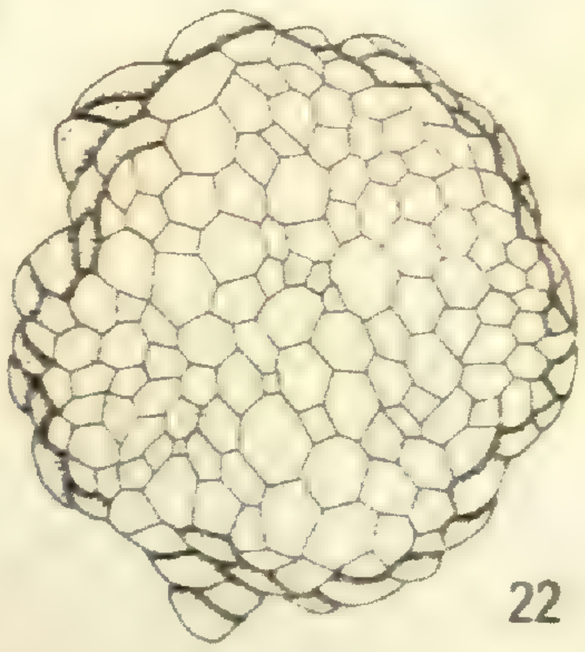

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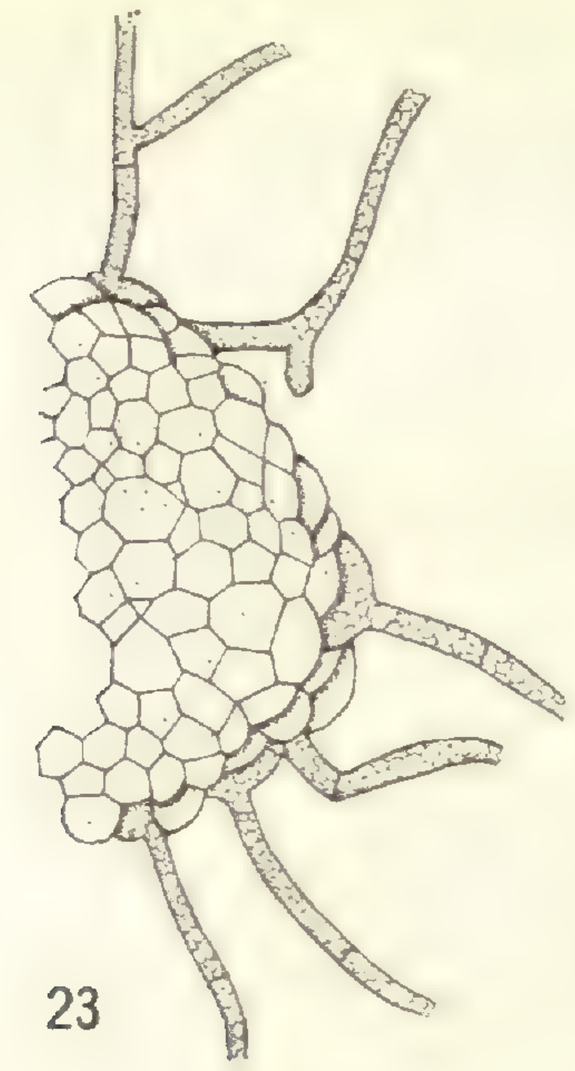

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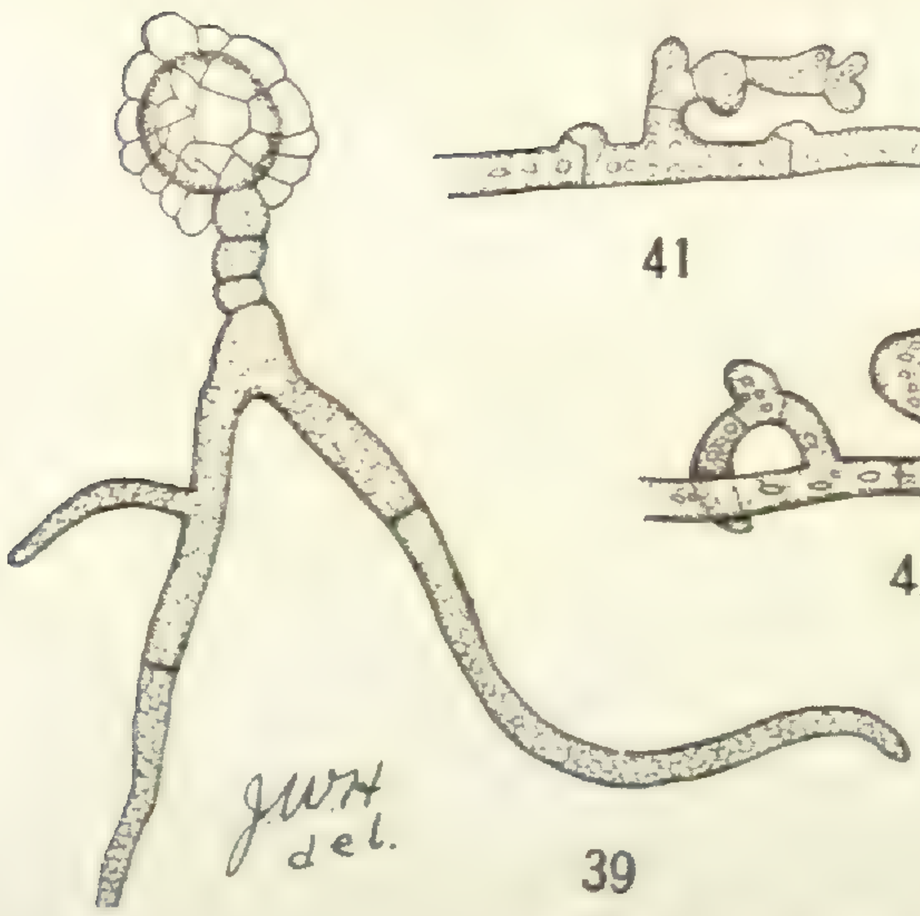

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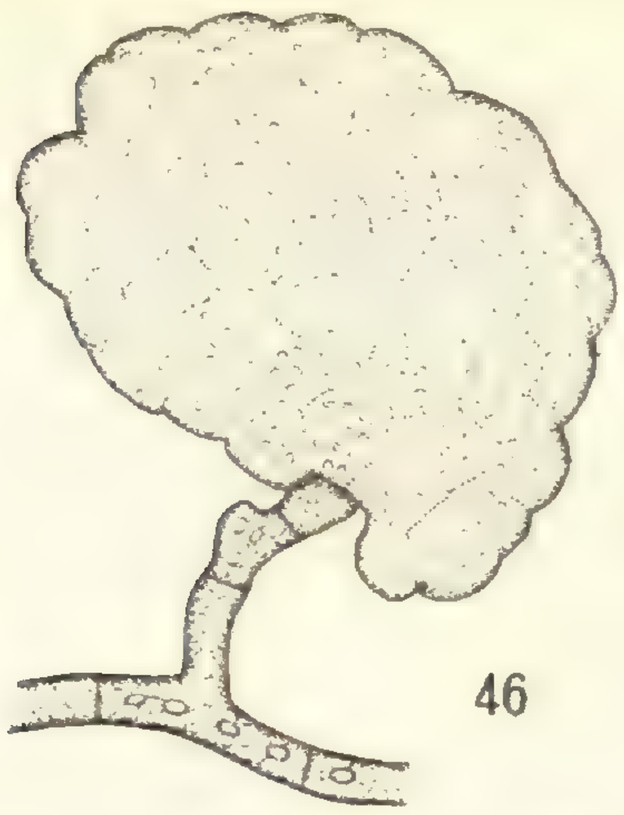

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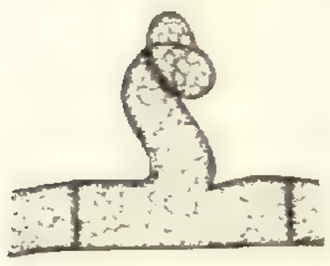

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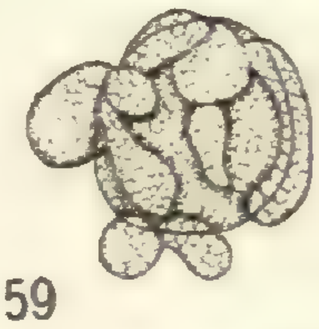

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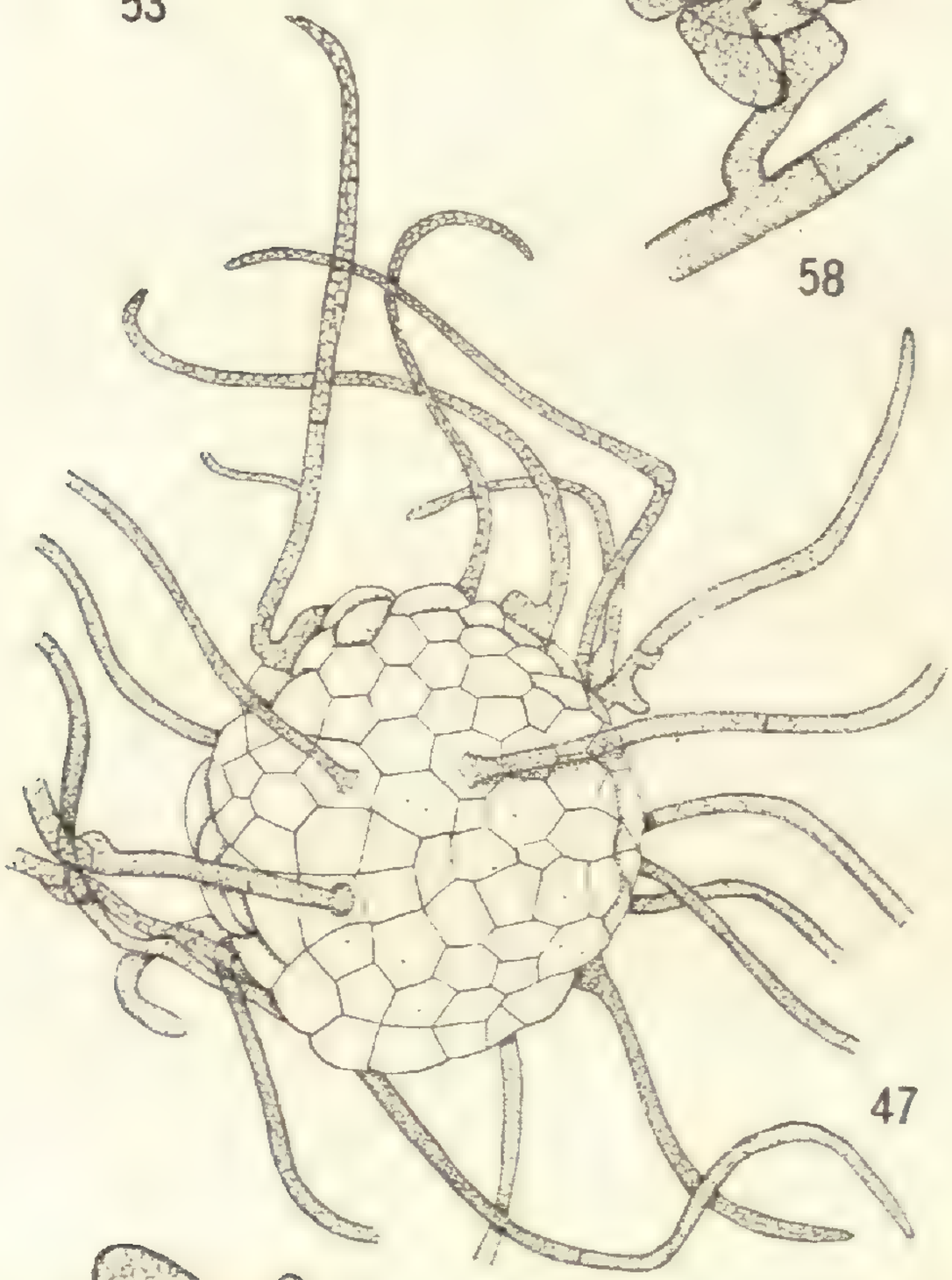

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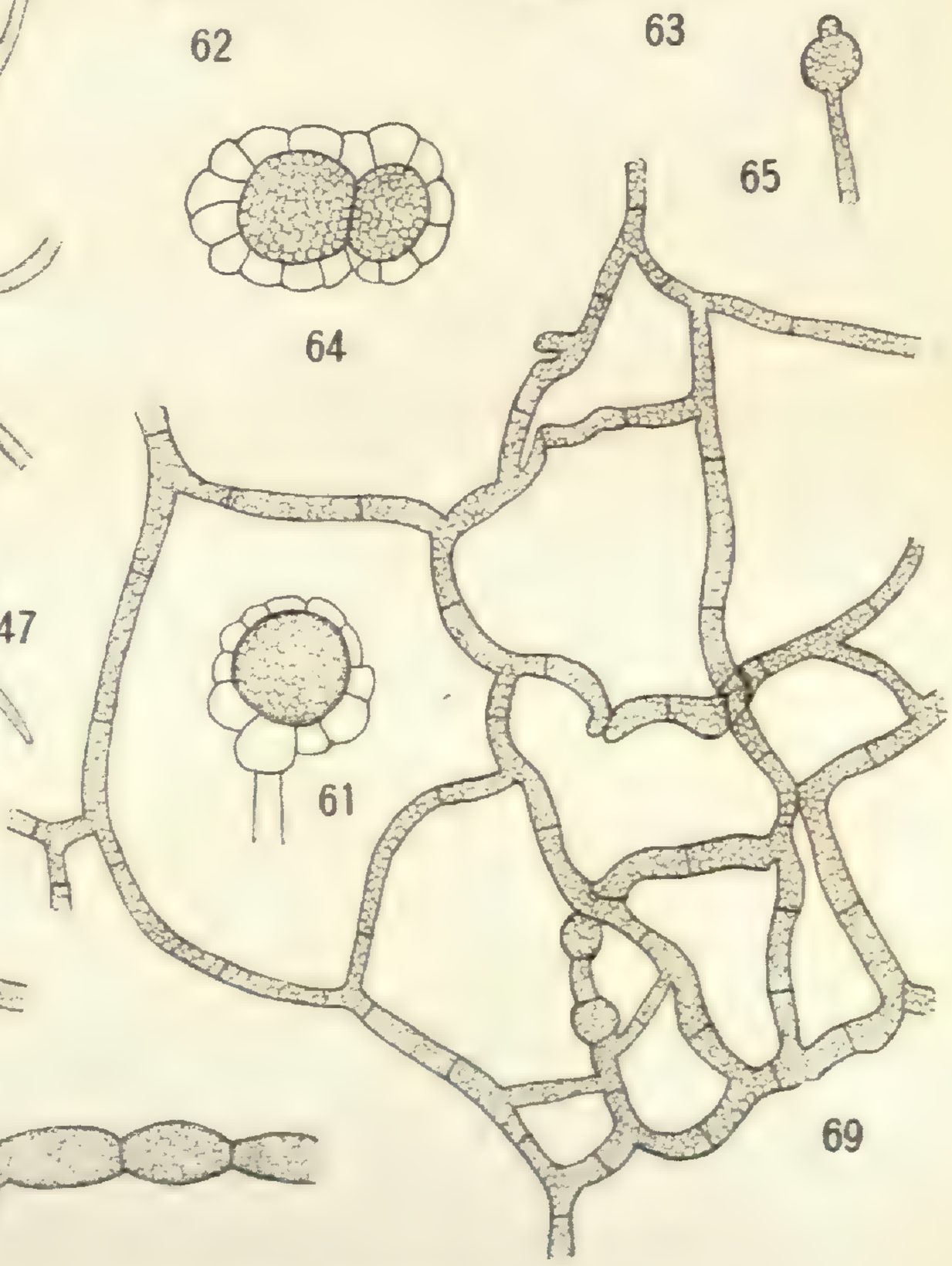

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HOTSON on BULBIFEROUS FUNGI

CRYOSCOPIC DETERMINATIONS ON TISSUE FLUIDS OF PLANTS OF JAMAICAN COASTAL DESERTS[1]

J. ARTHUR HARRIS AND JOHN V. LAWRENCE

Introduction

PURPOSE OF STUDY.—In a memoir recently published[2] we have discussed in detail the reasons for considering the physico-chemical properties of vegetable saps a subject of real importance in ecology and phytogeography, and have reinforced the arguments advanced by series of determinations showing distinct differences in the osmotic pressure, or osmotic concentration, as some prefer to call it, of leaf sap from plants growing in different local habitats in the Arizona deserts. A comparison of these determinations with a series made in the more mesophytic region of the Station for Experimental Evolution[3] demonstrated a conspicuous differentiation of the Tucson and Cold Spring Harbor regions with respect to the osmotic concentration of the tissue fluids of the constituent species. In view of the conspicuous differences established between these two floras, it seemed desirable to select a forested region of as uniformly distributed and as nearly maximum rainfall as possible for comparison with the areas already studied. Thus we hoped to approximate the extreme values of osmotic concentration to be found in xerophytic and hygrophytic regions. For such a study the montane rain forest of the island of Jamaica, recently described by SHREVE,[4] seemed the most suitable locality. We therefore spent a period of several weeks during the winter and spring months

[1] Studies carried out by the Department of Botanical Research and the Department of Experimental Evolution of the Carnegie Institution of Washington, with the collaboration of the New York Botanical Garden.

[2] HARRIS, J. ARTHUR, and LAWRENCE, JOHN V., with the co-operation of GORTNER, R. A., The cryoscopic constants of expressed vegetable saps as related to local environmental conditions in the Arizona deserts. Phys. Researches 2:1–49. 1916.

[3] HARRIS, J. ARTHUR, LAWRENCE, JOHN V., and GORTNER, R. A., On the osmotic pressure of the juices of desert plants. Science N.S. 41:656–658. 1915.

[4] SHREVE, F., A montane rain forest. A contribution to the physiological plant geography of Jamaica. Publ. Carnegie Inst. Wash. 199. 1914.

of 1915 in a study of the osmotic concentration of the tissue fluids of the plants of the montane region. The results of this study will be published later. Fortunately, while in Jamaica we were also able to visit the remarkable coastal deserts of the southern shore. It seemed to us highly desirable to secure as large a series of determinations as possible upon the species constituting their flora for comparison with the observations already made in the Arizona deserts in the neighborhood of the Desert Laboratory. Our purpose in this paper, therefore, is to present a considerable series of novel physiological data on the plants of the desert area of the southern coast of Jamaica; to compare the flora in this regard with that of the southern Arizona deserts and of some other localities; and to hazard some suggestions concerning biological factors immediately underlying certain of the differences observed in various species of the coastal region.

CHARACTERISTICS OF DESERTS INVESTIGATED.—Lying as it does in the center of the Carribean Sea, the island of Jamaica intercepts the trade winds in a way to cause a pronounced differentiation in its climatic conditions. This is especially true on the narrow eastern end, where the Blue Mountains, attaining a height of nearly 7500 feet, separate two narrow coast plains. At Port Antonio, at sea level on the northern coast of the island, the mean annual rainfall averages more than 130 inches. At Kingston, at sea level on the southern coast of the island, precipitation is on the average less than 38 inches per year. Temperature and insolation characteristic of sea level at 18° N. latitude coupled with local peculiarities of the substratum have here resulted in a conspicuously xerophytic type of vegetation.

As limited by SHREVE[5], the desert fringes the southern coast of the island from the mouth of the Cane River, just east of Kingston, for a distance of about 70 miles to the Pedro Bluffs. Its greatest area is found in the Healthshire Hills, in the vicinity of Port Henderson, and in Portland Ridge.

As SHREVE points out, the rainfall is capable of supporting a savanna of coarse grasses and large mimosaceous trees wherever the soil is deep, as in the vicinity of Spanish Town, Porus, and May

[5] SHREVE, F., The coastal deserts of Jamaica. Plant World 13:129–134. 1910.

Pen. The desert is confined to the limestone areas which have an extremely rough surface, with layers or shallow pockets of soil which are not capable of retaining moisture or of deriving it by capillarity, and to the finely ground substratum of the coastal flats. The proximity of the sea and other factors maintain a high relative humidity. Atmometer readings by SHREVE indicate that the evaporation rates here and at Hope Gardens, which is some 6 miles inland and behind a low ridge of hills, are not very different.

All of our collections were made in the immediate vicinity of Port Henderson, a point easily accessible from Spanish Town, where it was possible to carry out the laboratory phases of the work, and which afforded access to both the rocky limestone hills and the coastal flats. Because of military restrictions, made with great courtesy, we were unable to visit all parts of the region. Probably distribution of the collections over a wider area would have modified but little the conclusions here drawn, although it might have increased the number of species upon which determinations are based.

The area considered comprises open beach, a mangrove swamp, a highly saline tract of mud flats practically free of vegetation, somewhat higher-lying flats of finely ground detrital material, and rocky limestone hills, the soil of which is relatively incapable of retaining water.

The determinations which we made on the plants of the open beach and on those of the mangrove swamp are reserved for a discussion of the sap properties of strand and mangrove swamp species, to be published later when data for other habitats (many of which have already been collected) are ready. The vegetation of the exceedingly saline mud flats is practically limited to the two well known halophytes *Batis maritima* and *Sesuvium Portulacastrum*, of which the former is much the more common, and the two mangroves *Avicennia nitida* and *Laguncularia racemosa*, which occur on the edges of the area. The determinations from this area are also omitted for the present. We restrict ourselves, therefore, to a discussion of the floras of the coastal flats and of the dry hills.

At the time of our visits, in the midwinter and early spring seasons, ephemerals were not seen. Practically all of our determinations are based upon sclerophyllous arborescent or suffrutescent

species, or upon cacti. Here, as is generally the case in desert regions, the classification of the plants with respect to growth form presents considerable difficulty. Trees are shrublike in stature and shrubs are correspondingly reduced in size. In spots where the soil is deeper or more retentive of moisture the size of the individuals may be much greater.

Describing the vegetation in terms of the species upon which we were able to secure determinations, we may note that the vegetation of the coastal flats is made up chiefly of a mesquite tree *Prosopis juliflora*, and a columnar cactus *Lemairocereus Hystrix*. Other trees or shrubs are *Caesalpinia vesicaria*, *Capparis cynophallophora*, *C. ferruginea*, and *Guaiacum officinale*. Our lists show determinations for 7 species of cacti. In addition to these, *Sesuvium Portulacastrum*, *Batis maritima*, and in places *Bromelia Pinguin* are abundant. On the rocky hillsides the more truly arborescent forms are *Bauhinia divaricata*, *Caesalpinia vesicaria*, *Canella Winterana*, *Capparis ferruginea*, *Cassia emarginata*, *Ichthyomethia Piscipula*, *Melicocca bijuga*, *Prosopis juliflora*, *Sarcomphalus Sarcomphalus*, *Schoepfia chrysophylloides*, and *Tamarindus indica*. The shrubs are *Chiococca alba*, *Croton flavens*, *Hypelate trifoliata*, *Lantana crocea* (?), *Morinda Roioc*, *Solanum bahamense*, and *Turnera ulmifolia*. The smaller ligneous species are the dwarf shrubs or half shrubs *Achyranthes halimifolia*, *Lantana reticulata*, and *Jatropha gossypifolia*, and the twiners *Echites Echites* and *Phillivertella clausa*. The only monocotyledonous plant from which a determination was secured was *Bromelia Pinguin*. The only herbaceous succulent noted was *Bryophyllum pinnatum*.

The cacti may also occur on the rocky hills, but in the immediate vicinity of Port Henderson the flora is almost exclusively of small trees and shrubs.

There are but few species in our series of determinations common to the two habitats. These are *Achyranthes halimifolia*, *Caesalpinia vesicaria*, *Capparis ferruginea*, *Jatropha gossypifolia*, and *Prosopis juliflora*.

METHODS.—The very simple technique used in making the determinations has been described in detail elsewhere.[6] Samples

[6] GORTNER, R. A., and HARRIS, J. ARTHUR, Notes on the technique of determining the depression of the freezing point. Plant World 17:49–53. 1914.

of tissue were collected in test tubes of about 100 cc. capacity and taken to the laboratory for freezing by immersion for several hours in an ice and salt mixture, in order to avoid errors in the extraction of sap as noted by DIXON and ATKINS[7] and ourselves.[8] The sap was then extracted by pressure in a small heavily tinned press bowl with a powerful hand screw. After filtering, the freezing-point lowering of the sap was determined by the use of a thermometer graduated in hundredths of degrees with divisions sufficiently large to permit reading approximately to thousandths of degrees.

In some instances a cloudiness or flocculent precipitate similar to that described by GORKE[9] was observed when the sap approached the freezing point or passed it in undercooling. We had no facilities for any investigation of these substances, but believe their pressure does not greatly, if at all, influence our results.

The measurements are recorded in degrees depression (Δ) corrected for undercooling and in atmospheres pressure (P) from a table published elsewhere.[10] The fact that a number of the determinations exceeded the range of the table as originally printed has led to the publication of a supplementary one.[11]

Presentation and analysis of data

In the following protocol the values to the extreme right opposite the species names are (whenever possible) averages. These averages are designated by bars. The individual readings upon which they are based, with their dates of collection, are entered below the species, except in the cases in which only a single determination is available and must serve, instead of an average, to represent the species.

[7] DIXON, H. H., and ATKINS, W. R. G., Osmotic pressures in plants. I. Methods of extracting sap from plant organs. Sci. Proc. Roy. Dublin Soc. N.S. **13**:422–433. 1913; also in notes from Bot. Sch. Trin. Coll. Dublin **2**:154–172. 1913.

[8] GORTNER, R. A., LAWRENCE, JOHN V., and HARRIS, J. ARTHUR, The extraction of sap from plant tissues by pressure. Biochem. Bull. **5**:139–142. *pl. 1.* 1916.

[9] GORKE, H., Über chemische Vorgänge beim Erfrieren der Pflanzen. Landwirthsch. Versuch. Stat. **65**:149–160. 1906.

[10] HARRIS, J. ARTHUR, and GORTNER, R. A., Note on the calculation of the osmotic pressure of expressed vegetable saps from the depression of the freezing point, with a table for the values of P for $\Delta = 0.001°$ to $\Delta = 2.999°$. Amer. Jour. Bot. **1**:75–78. 1914; reprinted in MATTHEW'S *Physiological Chemistry*.

[11] HARRIS, J. ARTHUR, An extension to 5.99° of tables to determine the osmotic pressure of expressed vegetable saps from the depression of the freezing point. Amer. Jour. Bot. **2**:418–419. 1915.

A. THE COASTAL FLATS

The following determinations were made on the sap extracted from the leaves of the small more or less sclerophyllous trees.

Caesalpinia vesicaria L. ..... $\overline{\Delta}=2.95$, $\overline{P}=35.4$
January 25, $\Delta=2.91$, $P=34.9$
March 26, $\Delta=3.08$, $P=37.0$
March 30, $\Delta=2.87$, $P=34.4$

Capparis cynophallophora L. (*C. jamaicensis* Jacq.) ..... $\overline{\Delta}=3.76$, $\overline{P}=45.0$
January 30, $\Delta=3.87$, $P=46.4$
April 2, $\Delta=3.64$, $P=43.6$

Capparis ferruginea L. ..... $\overline{\Delta}=4.12$, $\overline{P}=49.3$
January 25, $\Delta=4.10$, $P=49.1$
March 30, $\Delta=4.13$, $P=49.4$

Guaiacum officinale L. ..... $\overline{\Delta}=4.35$, $\overline{P}=52.1$
January 25, $\Delta=4.48$, $P=53.6$
March 26, $\Delta=4.22$, $P=50.5$

Prosopis juliflora (L.) DC. ..... $\overline{\Delta}=2.53$, $\overline{P}=30.3$
March 30, $\Delta=2.42$, $P=29.1$
April 2, $\Delta=2.63$, $P=31.5$

Three species which may be classified as dwarf shrubs or half shrubs gave

Achyranthes halimifolia Lam. ..... $\overline{\Delta}=2.86$, $\overline{P}=34.3$
January 22, $\Delta=3.23$, $P=38.7$
January 25, $\Delta=2.48$, $P=29.8$

Batis maritima L. ..... $\overline{\Delta}=4.18$, $\overline{P}=50.0$
January 22, $\Delta=4.18$, $P=50.0$
January 25, $\Delta=3.84$, $P=46.0$
March 26, $\Delta=4.58$, $P=54.8$
March 30, $\Delta=4.12$, $P=49.3$

Jatropha gossypifolia L. ..... $\overline{\Delta}=1.17$, $\overline{P}=14.1$
January 25, $\Delta=1.24$, $P=14.9$
January 30, $\Delta=1.10$, $P=13.2$

Our visit was not made during the time of the development of ephemeral plants. The only herbaceous form which we secured was the well known halophyte *Sesuvium*.

Sesuvium Portulacastrum L. ..... $\overline{\Delta}=2.86$, $\overline{P}=34.3$
January 30, $\Delta=3.28$, $P=39.3$
January 30, $\Delta=4.03$, $P=48.3$
March 26, $\Delta=4.17$, $P=49.9$
March 26, $\Delta=1.94$, $P=23.3$
March 30, $\Delta=2.11$, $P=25.4$
April 2, $\Delta=1.63$, $P=19.5$

A portion of the foregoing species are sclerophyllous and a portion are succulent-leaved plants. The tissues of the Cactaceae, which are the dominant forms on the coastal flats, yield fluids giving the following values:

Cactus Melocactus L.

January 22, for cortex, $\Delta=0.40$, $P=4.9$
for pith, $\Delta=0.49$, $P=5.9$
March 30, $\Delta=0.46$, $P=5.5$
April 2, $\Delta=0.57$, $P=6.9$

Cephalocereus Swartzii (Griseb.) Britton and Rose

March 30, for cortex, $\Delta=0.59$, $P=7.1$
for pith, $\Delta=0.70$, $P=8.5$
April 2, for cortex, $\Delta=0.59$, $P=7.1$
for pith, $\Delta=0.69$, $P=8.3$

Harrisia gracilis (Mill.) Britton

March 26, for cortex, $\Delta=0.53$, $P=6.3$

Hylocereus triangularis (Mill.) Britton and Rose

January 25, $\Delta=0.48$, $P=5.8$

Lemairocereus Hystrix (Solm Byck) Britton and Rose

for cortex, $\Delta=0.64$, $P=7.7$
for pith, $\Delta=0.75$, $P=9.0$
January 25, for cortex, $\Delta=0.44$, $P=5.2$
for pith, $\Delta=0.64$, $P=7.7$
March 26, $\Delta=0.64$, $P=7.6$
March 30, for cortex, $\Delta=0.53$, $P=6.3$
for pith, $\Delta=0.57$, $P=6.9$
April 2, for cortex, $\Delta=0.80$, $P=9.7$
for pith, $\Delta=0.76$, $P=9.1$

Opuntia Dillenii (Ker Gawl.) Haw.

January 25, $\Delta=0.57$, $P=6.8$
March 30, $\Delta=0.75$, $P=9.0$
April 2, $\Delta=0.69$, $P=8.3$

Opuntia spinosissima Mill.

January 25, $\Delta=0.57$, $P=6.8$
March 26, $\Delta=0.78$, $P=9.4$
March 30, $\Delta=0.72$, $P=8.6$
April 2, $\Delta=0.93$, $P=11.1$

The only monocotyledonous plant studied was the terrestrial *Bromelia*, which may be included here.

Bromelia Pinguin L.....March 26, $\Delta=0.63$, $P=7.6$

B. THE ROCKY HILLS

The classification of the plants from the rocky hills into trees, shrubs, and other growth forms has been indicated in the foregoing introductory section. Here, therefore, we merely give the results of the determinations in alphabetical order.

Achyranthes halimifolia Lam. . . . . $\bar{\Delta}=2.83$, $\bar{P}=33.9$
March 26, $\Delta=3.16$, $P=37.9$
March 30, $\Delta=2.49$, $P=29.9$

Bauhinia divaricata L. . . . . $\bar{\Delta}=3.04$, $\bar{P}=36.5$
January 27, $\Delta=3.10$, $P=37.2$
January 30, $\Delta=2.98$, $P=35.8$

Bromelia Pinguin L. . . . . $\bar{\Delta}=0.58$, $\bar{P}=7.0$
March 30, $\Delta=0.52$, $P=6.3$
April 2, $\Delta=0.64$, $P=7.7$

Bryophyllum pinnatum (Lam.) Kurz . . . . . $\bar{\Delta}=0.44$, $\bar{P}=5.5$
March 26, $\Delta=0.49$, $P=5.9$
March 30, $\Delta=0.37$, $P=4.5$
April 2, $\Delta=0.50$, $P=6.0$

Caesalpinia vesicaria L. . . . . January 27, $\Delta=2.26$, $P=27.2$

Canella Winterana (L.) Gaertn. . . . . $\bar{\Delta}=3.18$, $\bar{P}=38.1$
January 27, $\Delta=3.29$, $P=39.5$
January 30, $\Delta=3.06$, $P=36.7$

Capparis ferruginea L. . . . . $\bar{\Delta}=3.58$, $\bar{P}=42.9$
January 30, $\Delta=3.50$, $P=41.9$
March 26, $\Delta=3.66$, $P=43.8$

Cassia emarginata L. . . . . $\bar{\Delta}=1.97$, $\bar{P}=23.6$
January 27, $\Delta=1.99$, $P=23.9$
January 30, $\Delta=1.94$, $P=23.3$

Chiococca alba (L.) Hitch. . . . . January 25, $\Delta=3.64$, $P=43.6$

Croton flavens L. . . . . January 27, $\Delta=1.47$, $P=17.7$

Echites Echites (L.) Britton (*Echites umbellata* Jacq.)
January 27, $\Delta=1.78$, $P=21.4$

Hypelate trifoliata Sw. . . . . $\bar{\Delta}=2.34$, $\bar{P}=28.1$
January 30, $\Delta=2.30$, $P=27.6$
March 30, $\Delta=2.38$, $P=28.6$

Ichthyomethia Piscipula (L.) Hitch. . . . . March 30, $\Delta=1.49$, $P=18.0$

Jatropha gossypifolia L. . . . . January 30, $\Delta=1.02$, $P=12.3$

Lantana crocea Jacq.? . . . . . March 26, $\Delta=1.60$, $P=19.2$

Lantana reticulata Pers. . . . . January 27, $\Delta=2.14$, $P=25.7$

Melicocca bijuga L. . . . . $\bar{\Delta}=1.87$, $\bar{P}=22.4$
January 30, $\Delta=1.73$, $P=20.8$
March 30, $\Delta=1.73$, $P=20.8$
April 2, $\Delta=2.14$, $P=25.7$

Morinda Roioc L. ..... $\overline{\Delta}=1.76$, $\overline{P}=21.2$
March 26, $\Delta=1.77$, $P=21.3$
March 26, $\Delta=1.76$, $P=21.1$
March 30, $\Delta=1.84$, $P=22.1$
April 2, $\Delta=1.68$, $P=20.2$
Philibertella clausa (Jacq.) Vail. ..... January 27, $\Delta=1.51$, $P=18.2$
Prosopis juliflora (L.) D.C. ..... January 27, $\Delta=2.69$, $P=32.3$
Sarcomphalus Sarcomphalus (L.) (*Sarcomphalus laurinus* Griseb.)
January 27, $\Delta=1.63$, $P=19.6$
Schoepfia chrysophylloides (Rich.) Planch ..... $\overline{\Delta}=2.79$, $\overline{P}=33.5$
January 27, $\Delta=2.52$, $P=30.2$
January 30, $\Delta=2.66$, $P=32.0$
March 26, $\Delta=2.93$, $P=35.1$
April 2, $\Delta=3.06$, $P=36.7$
Solanum bahamense L. ..... $\overline{\Delta}=1.98$, $\overline{P}=23.8$
January 27, $\Delta=1.85$, $P=22.2$
January 30, $\Delta=1.61$, $P=19.4$
March 26, $\Delta=2.25$, $P=27.0$
March 30, $\Delta=2.12$, $P=25.4$
April 2, $\Delta=2.09$, $P=25.1$
Tamarindus indica L. ..... $\overline{\Delta}=1.75$, $\overline{P}=21.0$
January 30, $\Delta=1.76$, $P=21.2$
March 26, $\Delta=1.89$, $P=22.7$
March 30, $\Delta=1.72$, $P=20.6$
April 2, $\Delta=1.63$, $P=19.6$
Turnera ulmifolia L. ..... January 25, $\Delta=3.39$, $P=40.7$

Analysis of data

In the analysis of these data the first step is to put on one side the two species with more or less succulent leaves, *Bromelia Pinguin* and *Bryophyllum pinnatum*, and the cacti. These show low concentrations of about 6–9 atmospheres. They are not at all comparable with the other forms investigated in these deserts and elsewhere and will be discussed separately on a subsequent page.

Of the thin-leaved forms, *Jatropha gossypifolia* has a thickened, almost succulent stem. It is a form much more characteristic of the coastal flats than of the rocky hillsides. The rather tender leaves yield a sap of lower concentration than that of any other thin-leaved species.

AVERAGE CONCENTRATION IN COASTAL DESERTS.—As a preliminary to any further analysis of these data the average values for the two habitats and the different growth forms must be obtained.

For the 5 arborescent species of the coastal flats the general average is given by

Caesalpinia	$\overline{\Delta}=2.95$,	$\overline{P}=35.4$
Capparis	$\overline{\Delta}=3.76$,	$\overline{P}=45.0$
Capparis	$\overline{\Delta}=4.12$,	$\overline{P}=49.3$
Guaiacum	$\overline{\Delta}=4.35$,	$\overline{P}=52.1$
Prosopis	$\overline{\Delta}=2.53$,	$\overline{P}=30.3$
General average	3.542	42.42

The 3 species of the coastal flats which have been classified as dwarf shrubs differ greatly in concentration. *Achyranthes* is a rather hard-leaved halophyte which does not penetrate to the most saline spots. It is characterized by a concentration of about 34 atmospheres as compared with about 50 atmospheres in the highly succulent *Batis maritima*, the sole species found in the more saline spots. *Sesuvium Portulacastrum* is characteristic of only the less saline portions of the flats, and shows a far lower average concentration, although some of the individual values attain about the average for *Batis*.

The actual averages are: mean depression, 2.737°; mean concentration, 32.80 atmospheres.

For the more truly arborescent species of the rocky slopes the values are:

Bauhinia	$\overline{\Delta}=3.04$,	$\overline{P}=36.5$
Caesalpinia	$\overline{\Delta}=2.26$,	$\overline{P}=27.2$
Canella	$\overline{\Delta}=3.18$,	$\overline{P}=38.1$
Capparis	$\overline{\Delta}=3.58$,	$\overline{P}=42.9$
Cassia	$\overline{\Delta}=1.97$,	$\overline{P}=23.6$
Ichthyomethia	$\overline{\Delta}=1.49$,	$\overline{P}=18.0$
Melicocca	$\overline{\Delta}=1.87$,	$\overline{P}=22.4$
Prosopis	$\overline{\Delta}=2.69$,	$\overline{P}=32.3$
Sarcomphalus	$\overline{\Delta}=1.63$,	$\overline{P}=19.6$
Schoepfia	$\overline{\Delta}=2.79$,	$\overline{P}=33.5$
Tamarindus	$\overline{\Delta}=1.75$,	$\overline{P}=21.0$
General average	2.388	28.6

The general average for the shrubs, half shrubs, and woody twiners of the rocky slopes is given by

Achyranthes	$\bar{\Delta}=2.83$, $\bar{P}=33.9$
Chiococca	$\Delta=3.64$, $P=43.6$
Croton	$\Delta=1.47$, $P=17.7$
Echites	$\Delta=1.78$, $P=21.4$
Hypelate	$\bar{\Delta}=2.34$, $\bar{P}=28.1$
Jatropha	$\Delta=1.02$, $P=12.3$
Lantana	$\Delta=1.60$, $P=19.2$
Lantana	$\Delta=2.14$, $P=25.7$
Morinda	$\bar{\Delta}=1.76$, $\bar{P}=21.2$
Philibertella	$\Delta=1.51$, $P=18.2$
Solanum	$\bar{\Delta}=1.98$, $\bar{P}=23.8$
Turnera	$\Delta=3.39$, $P=40.7$
General average	2.122 25.48

Thus the concentrations determined for the smaller forms are practically as large as those for the more truly arborescent species.

Combining all the ligneous perennials of the rocky slopes (that is, omitting from the whole series of determinations only *Bromelia* and *Bryophyllum*), we have for the general average of the species means or species constants: mean depression, 2.249°; mean concentration, 27.000 atmospheres.

Combining both arborescent and suffrutescent growth forms, excepting only the herbaceous *Sesuvium Portulacastrum*, *Bromelia*, *Bryophyllum*, and the cacti, the values for the 31 species means or constants of the two habitats recognized give the following averages: mean depression, 2.505°; mean concentration, 30.05 atmospheres. By including the herbaceous perennial *Sesuvium*, the averages for 32 species means or determinations is changed to $\bar{\Delta}=2.516$, $\bar{P}=30.18$.

COMPARISON OF CONSTANTS WITH THOSE FOR MESOPHYTIC REGIONS.—The first question to be answered in the analysis of these data is that concerning the relative values of osmotic concentration in the sap of desert and mesophytic plant organisms. Specifically, do the results of this study confirm those obtained by FITTING[12] in

[12] FITTING, H., Die Wasserversorgung und die osmotischen Druckverhältnisse der Wüstenpflanzen. Zeitschr. Bot. 3:209–275. 1911.

his plasmolytic studies of the plants of North African deserts and by ourselves in our cryoscopic determinations in the Arizona desert region? With an affirmative answer to this question, a second one concerning the closeness of agreement between the two desert areas so far investigated is open to discussion.

Comparisons of the constants for sap properties here secured with those for other regions must be drawn with care and in only a preliminary fashion. This is quite obvious because of the many factors which may influence the constants, but concerning which little or no quantitative data are at present available. For example, the determinations for the Arizona deserts are based on collections made during the period of spring vegetative activity following the winter and spring rains; those for the coastal deserts were made during the dry winter season. The collections made on Long Island and in St. Louis at the Missouri Botanical Garden comprise deciduous species whose leaves must have developed during the spring of the same year. The age of the leaves of the desert plants is often quite indeterminable. Bearing these limitations in mind and remembering that there are probably many others, we note first of all that in a general way the flora of the Port Henderson deserts is in excellent agreement with that of the Tucson region in showing a high concentration of the tissue fluids of its constituent species. The exceptions only emphasize the rule.

Thus comparing the Port Henderson averages for ligneous perennials with those tentatively drawn from unpublished data for trees and shrubs for the Cold Spring Harbor region,[13] we find

Cold Spring Harbor, 14.40 atmospheres
Jamaican coastal desert
Coastal flats only, 38.81 atmospheres
Rocky slopes only, 27.00 atmospheres
Flats and rocky slopes, 30.05 atmospheres.

[13] The averages given for both the Cold Spring Harbor and the Tucson series are means of determinations, not of species means. The difference is here quite immaterial. The Cold Spring Harbor means are based on determinations made in 1914 by GORTNER, LAWRENCE, and HARRIS. They will be replaced shortly by those representing not merely determinations made in 1914 but far more extensive work by LAWRENCE and HARRIS in 1915 and subsequent work by HARRIS. The field work has been done for a summer series from the Arizona deserts, but the data cannot be completely worked up for some months.

It is idle to go further into these comparisons. It is clear that the ligneous plants of the Jamaican coastal desert, those of the rocky hills as well as of the more or less saline flats, are characterized by concentration of tissue fluids about twice as great as those of the Cold Spring Harbor region.

The extensive series of species studied by OHLWEILER[14] suffer from the disadvantage (in relation to the present paper) of being assembled from their natural habitats and grown in a Botanical Garden. All, however, are forms capable of growth in the open at St. Louis. These show a range of from about 7 to about 24 atmospheres. The average value of the 90 determinations is 14.96 atmospheres. Thus, OHLWEILER's St. Louis series agrees very closely with our own preliminary average for Long Island habitats. Here again the values are only about half as high as those determined in the coastal deserts.

COMPARISON OF CONSTANTS WITH THOSE FOR TUCSON REGION.—Turning to averages for a comparison of the concentration of the sap of the Jamaican coastal and the Arizona desert floras, the results for ligneous perennials only are: Arizona series, 24.97 atmospheres; Jamaican series, 30.05 atmospheres. Apparently concentration is somewhat greater in the Jamaican series. If the comparison between the two desert areas is to be drawn on a more analytical basis, it may be noted that the values determined for the trees of the coastal flats are of the same order of magnitude as those derived from the species of *Atriplex* examined in the Arizona salt spots. For example:

Atriplex canescens	$P=39.5$
Atriplex canescens	$P=67.5$
Atriplex canescens angustifolia	$P=32.8$
Atriplex polycarpa	$P=52.0$

In the Jamaican coastal deserts the trees and shrubs from the rocky slopes show concentrations lower than those of the coastal flats. In the Arizona deserts the plants of the rocky slopes show far lower osmotic concentrations than do those of the salt spots. Comparing Arizona and Jamaican rocky slopes the results are:

[14] OHLWEILER, W. W., The relation between the density of cell saps and the freezing point of leaves. Ann. Rept. Mo. Bot. Gard. **23**:101–131. *pl. 6.* 1912.

Port Henderson region, 27.00 atmospheres; Tucson region, 22.01 atmospheres.

With the exception of the salt spots, the bajada slopes of the Tucson region show the highest concentration. Comparing with the rocky slopes of the coastal region, the results are: Port Henderson rocky slopes, 27.00 atmospheres; Tucson region, bajada, 30.34 atmospheres.

Because of seasonal differences it is undesirable to attempt to analyze too closely the differences between the two desert areas. Such could be done if determinations upon the coastal deserts immediately subsequent to a rainy season were available. Until such data are at hand and until our determinations for the summer flora of the Arizona deserts are ready for publication, it is premature to discuss the matter further than to say that both of these regions show concentrations far higher than do those of mesophytic habitats, and that they are in good general agreement between themselves.

OSMOTIC CONCENTRATION IN THE CACTI.—From the floristic standpoint the most striking feature of these coastal deserts is the remarkable growth of arborescent cacti in immediate proximity to dense mangrove swamps. From the physiological standpoint the most remarkable result of these studies is the demonstration that the fluids of these cacti have about the same concentration as those of other desert regions.

The 28 determinations made on the sap of the 7 species belonging to the 6 genera of cacti show a range of $\Delta = 0.40$ to $\Delta = 0.93$, or $P = 4.9$ to $P = 11.1$, with an average for the series of $\bar{\Delta} = 0.626$ and $\bar{P} = 7.52$. Yet these cacti are growing in the same substratum as sclerophyllous arborescent species with an average concentration for the species of $\bar{\Delta} = 3.54$ and $\bar{P} = 42.4$. Much of the cactus-covered area has a dense undergrowth of *Batis maritima*, which has an average of $\bar{\Delta} = 4.18$, $\bar{P} = 50.0$. *Sesuvium*, which sometimes occurs but is not so abundant as *Batis* among the cacti, has sap averaging $\bar{\Delta} = 2.60$, $\bar{P} = 31.2$. Better illustrations of the diverse reaction of two organisms to the same general environmental situation could hardly be found. These results are in close agreement with the findings of those who have worked on the cacti in other regions.

As early as 1905 CAVARA[15] investigated a series of cacti by the freezing-point lowering method and gave values not very dissimilar from our own. Sap was extracted from untreated tissue. This may result in abnormally low values of the measures of osmotic concentration.

MACDOUGAL and CANNON[16] have estimated the following concentrations in atmospheres for sap of cacti at 25° C: *Carnegiea gigantea*, 6.78; *Echinocactus Wislizenii*, 5.72; *Opuntia Blakeana*, 8.88 and *O. versicolor*, 11.98.

It is interesting from the historical standpoint to note that cacti, which with certain other succulents are quite anomalous among desert plants, were perhaps the first to be considered in relation to the problem of the dependence of absorption of water by desert plants upon higher osmotic pressure of their sap. Thus LIVINGSTON[17] concluded, from determinations by the freezing-point, boiling-point, and tissue curvature methods, that the saps of *Cereus*, *Echinocactus*, and *Opuntia* "exhibit osmotic pressures no higher than those commonly found in plants of the humid regions. For these cacti at least, therefore, adaptation to desert conditions is not manifest in increased concentration of the cell sap."

From the foregoing account we may say that the cacti of the Jamaica coast exhibit sap concentration of roughly the same order of magnitude as do those of other regions. Possibly they are somewhat higher than those of purely non-saline localities, but until series in which standard methods of sap extraction have been employed are available from other habitats this cannot be asserted to be the case. Certainly the cacti, with *Bromelia* and *Bryophyllum*, are conspicuous exceptions to the general rule of high osmotic concentration in these coastal forms. To this point we shall recur later.

Results

In the foregoing paragraphs we have shown that the sap of the plant species of the Jamaican coastal deserts has an osmotic

[15] CAVARA, F., Risultati di una serie di ricerche crioscopiche sui vegetati. Cont. Biol. Veg. R. Ist. Bot. Palermo 4:41–80. 1905.

[16] MACDOUGAL, D. T., and CANNON, W. A., The conditions of parasitism in plants. Publ. Carnegie Inst. Wash. 129. 1910.

[17] LIVINGSTON, B. E., The relation of desert plants to soil moisture and evaporation. Publ. Carnegie Inst. Wash. 50. 1906.

concentration far higher than those of mesophytic regions, and quite equal to if not slightly higher than those of the winter vegetation of the Arizona deserts.

While determinations based on these species growing in other environments are as yet too few to justify detailed discussion, it seems most probable that the properties of their sap are due in part to the local conditions and not merely to the existence here of a series of species characterized by high concentration.[18]

In the few cases in which constants for a species were obtained from the coastal flats and from the rocky slopes, the values from the slopes are generally lower than those from the flats. Thus the single determination on *Caesalpinia vesicaria* from the slopes gives 27.2 atmospheres as compared with 34.4, 34.9, and 37.0 from the flats. *Capparis ferruginea* from the slopes gives 41.9 and 43.8 atmospheres as compared with 49.1 and 49.4 atmospheres when growing on the flats. *Jatropha gossypifolia* gives 12.3 atmospheres on the slopes as compared with 13.2 and 14.9 on the flats.

In the case of *Prosopis juliflora* and *Achyranthes halimifolia*, the result is uncertain. The two collections of *Achyranthes* from the slope gave 29.9 and 37.9 as compared with 29.8 and 38.7 atmospheres for the flats. *Prosopis* on the slopes yielded sap with a concentration of 32.3 atmospheres as compared with two readings of 29.1 and 31.5 from the flats.

To what extent the osmotic concentration of the sap of the sclerophyllous forms is influenced by the actual presence of salt in the leaves can only be determined by special methods. The leaves of some of the forms growing on the coastal flats, for example *Capparis ferruginea*, are perceptibly salty to the taste; others are not. It can hardly be doubted that the enormous variation in the concentration of the leaf fluids of such forms as *Batis maritima* and *Sesuvium Portulacastrum*, the leaves of which are practically reinforced water bags, is due primarily to electrolytes absorbed from the soil. The fact that the various cacti are here characterized by sap of low concentration, as when growing in true desert environ-

[18] A collection of the leaves of *Guaiacum officinale* from Spanish Town gave only $\Delta = 2.66$, $P = 31.9$ as compared with two constants each over 4° (50 atmospheres) in the coastal flats.

ments, indicates that the absorption of any considerable quantity of salts and their retention in solution is not a necessary result of existence in a saline substratum. Some physiologists have suggested that the high osmotic concentration of the fluids of desert plants is due primarily and directly to greater quantities of soluble material in the substratum than generally occurs in regions of higher rainfall. The validity of the conclusion is rendered highly improbable by the high concentrations demonstrated for the plants of the rocky hillsides.

While in general it is better to reserve hypotheses concerning the peculiarities of individual species until theoretical discussions of their relation to environmental factors can be replaced by inductions from actual quantitative data secured in the particular habitat under investigation, it may be useful to other workers, especially in the case of a problem requiring so many different kinds of specialized observation in a habitat not easily accessible to most botanists, to point out certain possible interpretations of the observed phenomena.

The question of greatest interest is that concerning the difference in behavior of the several species of the same habitat, say the coastal flats. For example, the leaves of *Prosopis* and *Caesalpinia* yield sap of a distinctly lower concentration than do those of *Guaiacum* and the two species of *Capparis*. *Jatropha gossypifolia* has sap of only about one-fourth of the concentration of that of *Batis maritima*, with which it is so generally associated. The cacti and the terrestrial bromeliad exhibit only a fraction of the freezing-point lowering shown by the hard and succulent leaves of the arborescent and suffrutescent species among which they are interspersed.

Any suggestion in interpretation of these phenomena must be purely tentative and be substantiated by, or discarded on the basis of, actual field studies. Those which are here called to the attention of ecologists are not at all speculative, but merely the result of an attempt to correlate the results of studies by a number of specialists in the various fields of desert botany.

Sesuvium Portulacastrum and *Batis maritima* are both species with highly succulent leaves. In both, the high osmotic concentration

of the leaf sap must be due primarily to electrolytes absorbed directly from the substratum. The difference between them, in so far as facts are available, seems to be an inherent physiological one. *Sesuvium* seems to be a form less tolerant of a highly concentrated soil solution than *Batis*. The local distribution of the two, therefore, is not at all comparable, and the distinctly higher concentration in the leaves of *Batis* is probably attributable to this fact.

The only suggestion which can be made concerning the anomalous position of *Prosopis* among the small trees is that it has a more deeply penetrating root system which taps underflow water, poor in solutes, derived by seepage from the neighboring limestone hills.[19] From the extensive observations in the deserts of southern Arizona it is known that the related species *Prosopis velutina* is characterized by deep root penetration. Thus SPALDING[20] and CANNON[21] both note the wide horizontal and the deep vertical distribution of the root system, which may reach a depth of 8 m. or over. CANNON[22] concludes that with uniform and penetrable substratum the species becomes a tree where the perennial ground water does not lie at a depth greater than 50 ft.

Such differences as exist between the concentration in the leaves of *Prosopis* and those of *Batis maritima* may be accounted for on the grounds of a much higher concentration of salts in the superficial soil layers.

It is interesting to note in this connection that *Prosopis juliflora* from the coastal deserts gives values of osmotic concentration in general agreement with *P. velutina* of the Arizona deserts. Thus two determinations made on young leaves in the spring of 1914[23] gave:

Santa Catalina Mountains, $\Delta = 2.08$, $P = 25.0$

Tucson Mountains, $\Delta = 2.33$, $P = 27.9$

[19] This suggestion was originally made by SHREVE (*loc. cit.*) to account for the presence of *Prosopis* in association with *Batis maritima* and other halophytes.

[20] SPALDING, V. M., Distribution and movements of desert plants. Publ. Carnegie Inst. Wash. 113. 1909.

[21] CANNON, W. A., The root habits of desert plants. Publ. Carnegie Inst. Wash. 131. 1911.

[22] CANNON, W. A., Some relations between root characters, ground water, and species distribution. Science, N.S. 37:420–423. 1913.

[23] Physiol. Researches 2:32. 1916.

Hitherto unpublished determinations made in the summer of 1916 by LEAMON and HARRIS give:

Santa Catalina bajada	
Edge of arroyo, July 6,	$\Delta = 2.63$, $P = 31.6$
Same tree, August 14,	$\Delta = 2.40$, $P = 28.8$
Upper bajada, July 6,	$\Delta = 2.87$, $P = 34.5$
Near San Xavier Mission	
Mesa-like slopes, July 24,	$\Delta = 2.51$, $P = 30.1$

Surely no one will venture to assert on the basis of the available data that the Jamaican *Prosopis juliflora* and the southwestern *P. velutina* are sensibly different in osmotic concentration.

With regard to the cacti, which have been shown elsewhere in this paper to have about the same concentration of tissue fluids as those found for this group growing in other habitats, the following points must be taken into account. The cacti are plants characterized by a deeply penetrating anchoring root system and a far-reaching superficially placed absorbing system. The evidences upon which this statement is based are chiefly those presented by CANNON in his large paper on the root habits of desert plants. If the coastal species agree in this regard with the forms which have been investigated, their absorbing organs are in contact with the actually dryest zone of the substratum during periods of severe drought, and with one physiologically dry, that is, characterized by a soil solution of high osmotic concentration, during periods of moderately abundant soil moisture.

Such are the conditions which result in the high concentration found in *Batis maritima*, and one might, at first thought, suppose that the cacti would also be subject to the same conditions. Two additional factors, however, are to be taken into account: (1) the cacti are organisms capable of rapid storage of water during transient periods of soil saturation,[24] and its persistent retention during

[24] The point is splendidly illustrated by two photographs of *Opuntia* published by CANNON (Amer. Nat. **40**:27–47. *figs.* 2–3. 1906). MACDOUGAL and SPALDING (The water balance of succulent plants. Publ. Carnegie Inst. Wash. 141. 1910) have dealt with the problem in greater detail. A number of other papers bearing more or less directly upon the general problem of water absorption and storage in the cacti have since appeared from the Desert Laboratory.

long periods of deprivation; (2) the rainfall in the Jamaican coastal desert region is not distributed uniformly throughout the year. During periods of heavy rainfall the salts would be highly diluted or even largely washed out of the superficial soil layers in which the absorbing roots of the cacti lie, thus permitting water intake in quantities quite sufficient to maintain the plant until conditions again become favorable for water absorption. Thus species may differ very greatly in the relationship of their sap properties to environmental factors. Two species may be rooted in the same substratum, but because of differences in root penetration or in their capacity for water absorption or retention in reality they may be living in very different environments, or reacting quite differently to the same environment.

Whether the hypotheses just advanced in explanation of the great diversity of the constants determined on the sap of particular species of plants growing in the same habitat be correct, can only be determined by intensive observational and experimental studies in the field. In the meantime they seem consistent with the available facts of desert plant physiology.

Recapitulation

In the present paper, which is one of a series on the physico-chemical properties of the tissue fluids of the plants of typical vegetations, we have presented the results of determinations of the freezing-point lowering of the tissue fluids of the plant species of the Jamaican coastal deserts; have compared the constants secured with those already available for the Arizona deserts and for meso-phytic habitats; and have offered tentative suggestions concerning the proximate causes of certain of the observed peculiarities of individual species.

The deserts investigated constitute a small area on the southern coast of the island, where not merely the reduction in the rainfall due to the interception of the trade winds by relatively high mountains, but peculiarities of the substratum, contribute to the rigor of conditions limiting plant growth.

Two sub-habitats have been recognized, low-lying coastal flats of finely ground detrital material, to a considerable extent impreg-

nated with salts, and rocky limestone hills incapable of retaining moisture or of deriving it by capillarity.

The vegetation of the coastal flats comprises a number of hard-leaved trees, among which is a mesquite very similar to that of the deserts of the southwestern United States, some thin and some succulent-leaved halophytes, and a number of genera and species of cacti which form a luxuriant stand. The vegetation of the rocky hills is of a more arborescent type, consisting chiefly of dwarfed broad-leaved trees with a number of small dwarf or half shrubs which have few purely structural characteristics which would ally them to desert plants.

Taken as a whole, the species of the Jamaican coastal deserts show a concentration of their tissue fluids quite as high as, if not slightly higher than, that of as nearly as possible comparable growth forms in the Arizona deserts. The concentration of the leaf sap of the ligneous forms averages about two or three times that demonstrated in mesophytic regions.

While the plants of the rocky slopes show high concentrations, higher indeed than do those of the rocky slopes of the Arizona deserts, their constants are distinctly lower than those of the species of the coastal flats.

The sap of the cacti has only a fraction of the osmotic concentration of that of the hard or succulent leaves of the trees and half shrubs among which they are rooted. The succulent *Bryophyllum pinnatum* and the terrestrial bromeliad *Bromelia Pinguin* show far lower concentrations than do the other species. Furthermore, *Prosopis juliflora* exhibits sap concentrations distinctly lower than those of certain other of the arborescent species. These form the extreme illustration of the fact that species of the same habitat show marked differences in sap properties. Suggestions concerning the underlying causes of such differences are offered.

STATION FOR EXPERIMENTAL EVOLUTION
COLD SPRING HARBOR, LONG ISLAND, N.Y.

A NEW METHOD OF STUDYING PERMEABILITY

S. C. Brooks

(WITH TWO FIGURES)

The writer[1] has shown the desirability of a study of permeability by some method which should be entirely independent of other methods, and yield data the interpretation of which need not depend upon any unverifiable assumptions. A method is here presented which seems to fulfil these requirements. It has proved to be exceedingly reliable; and the experiments point clearly to the errors previously made in the interpretation of the data secured by many methods, and to the validity of the conclusions based on the evidence of certain others.

Method

The method depends upon diffusion of salts or other substances through a diaphragm of living tissue. For this purpose fronds of one of the common kelps of the New England coast, *Laminaria Agardhii* (formerly identified as *L. saccharina*), proved to be extremely satisfactory material because of absence of air spaces in the tissue, ease of manipulation, resistance to adverse conditions, and especially because it was possible to secure thin sheets of tissue in which there were no wounded surfaces in contact with the solutions.

The method of experimentation was as follows. Sections of glass tubing of 18 mm. internal diameter were cut; one end of each piece was flared and the end ground flat. The resulting "cells" were either 2.5 cm. or 4 cm. in length, and were combined in pairs, each consisting of one long and one short cell (fig. 1, *A*, *B*). The unground end of the longer cell was closed by a rubber tube and pinchcock (fig. 1, *C*, *D*). Disks were cut from the fronds of *Laminaria* of such a size as nearly to cover the ground ends of the tubes.

[1] Brooks, S. C., Methods of studying the permeability of protoplasm salts. Bot. Gaz. 64:230–249. 1917.

In the experiments with living material the surface of these disks was quickly dried with filter paper, the disks (fig. 1, *E*) placed between the ground ends of a pair of cells, and the joint made tight with a stiff cement consisting of a mixture of vaseline and beeswax (fig. 1, *F*). Thus there were formed two cells separated by a diaphragm of *Laminaria* tissue. The cell supplied with the rubber tube and pinchcock (hereafter called the "lower cell") was then filled with solution and the pinchcock closed, care being taken that no air bubbles were included in the cell. The apparatus was then inverted and the upper cell filled with solution, covered to check evaporation (fig. 1, *G*), and set in a suitable support. During these operations each disk was in contact with the air less than two minutes, which was not sufficient to cause any appreciable drying-out of the tissue.

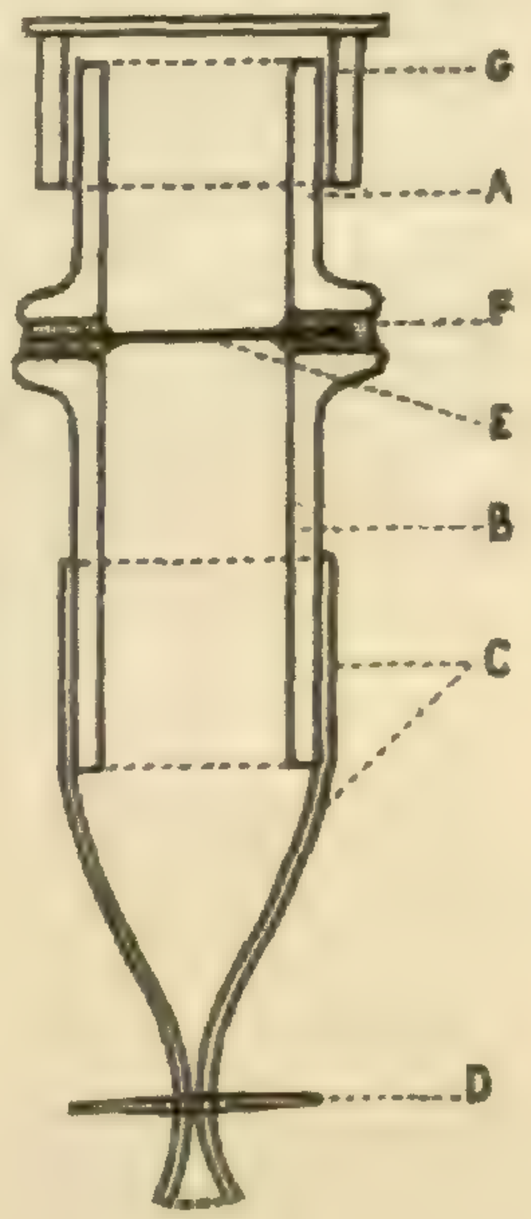

FIG. 1

In order to obtain dead tissue for experiments on the permeability of the intercellular substance, living disks were exposed, after cutting, to an atmosphere saturated with chloroform vapor at room temperature for 16–24 hours. They were next exposed to the air about one hour to allow the complete evaporation of any chloroform which remained in the tissue, and then placed in a large volume of sea water for about 24 hours to allow the establishment of equilibrium between the electrolytes of the sea water and those in the dead cells. At the end of this time the surface of the disks of tissue was dried with filter paper, and the apparatus set up as in the experiments with living material. Tissue which had died a natural death gave results in every way similar to those given by tissue killed in this manner.

The permeability of the tissue was shown by the rate of passage of salts through the diaphragm as shown by diminution of the difference of concentration between the solutions in the upper and lower cells. It is possible to measure rapidly, and with extreme accuracy, slight changes in the concentration of the solutions in either cell by determining the change in electrical conductivity. This method was therefore employed.

The solution used in the lower cells was either sea water or a pure salt solution of the same conductivity; while the upper cells contained a solution of half the concentration of that in the corresponding lower cell. Solutions of equal conductivity were used in order to facilitate comparison with the work of OSTERHOUT.[2]

Sources of error

In order to obtain accurate data, the following precautions were taken:

1. The solutions were made up with distilled water, which had a specific conductivity of about 2×10^{-6} ohms. The sodium chloride used was Baker's "analyzed"; the calcium chloride, Kahlbaum's; and the lanthanum nitrate, Eimer and Amend's "Tested Purity." For this work an error of 1 per cent in the concentration of the solutions was considered allowable.

2. In order to prevent dissolving of electrolytes from any part of the apparatus, the cells were made of Durox glass, and both cells and rubber thoroughly steamed immediately before each experiment. An apparatus of this type, set up with no *Laminaria* tissue, but with a thick layer of the vaseline-beeswax cement, and filled with distilled water, gave off only traces of electrolytes. The change in conductivity of the water in such a cell during 48 hours was equivalent to an increase of concentration of sodium chloride of less than 1×10^{-7} M. Dissolving of electrolytes from the apparatus has therefore no significance in the experiments.

3. It was necessary to eliminate the influence of temperature. As it was impracticable to conduct the experiments at constant temperature, the cells were placed outdoors, the temperature varying from -3° to $+9^{\circ}$ C. This amount of fluctuation produced no appreciable change in the rate at which salts passed through the tissue, and the low temperatures were exceedingly favorable to the maintenance of normal permeability.[3]

[2] Unpublished data of OSTERHOUT show that differences of osmotic pressure of the magnitude of those produced by the use of solutions of equal conductivity have little effect on the permeability of *Laminaria* during the length of time occupied by these experiments.

[3] *Laminaria* lives much longer when the temperature is low. While it may be kept alive under laboratory conditions several weeks at 0° C., it perishes rapidly at 24° C.

4. The *Laminaria* thallus is made up of masses of protoplasm (the cells) imbedded in a gelatinous intercellular substance. From this intercellular substance, in which the salts are present in the same concentration as in sea water, the salts will diffuse out into a surrounding medium, and will alter its conductivity if it be other than that of sea water. From the protoplasm, also, a similar diffusion may take place, which for convenience may be designated as "exosmosis."

That there is actual passage of salts through the tissue was shown by the fact that the conductivity of the more dilute solution always increased, while that of the more concentrated solution decreased to a corresponding degree. There was no appreciable change in the volume of either solution even during experiments whose duration was greater than 24 hours. The relative amounts of increase in the upper cell and of decrease in the lower cell, as found in the experiments, were in fair agreement with those calculated. If a given amount of salt passes from one salt solution to an equal volume of another solution having half the concentration of the first, the percentage of increase in the concentration of the latter will be double the percentage of decrease in the former. If there be a difference in volume between the two solutions, the change caused by the addition or removal of a given amount of salt will be inversely proportional to the volume. Thus, in one experiment the increase in concentration in the upper cell was 1 per cent per hour, while the decrease in the lower cell was 0.26 per cent per hour. Since the volume in the upper cell was 5.4 cc. as compared with 12.5 cc. in the lower, and the concentrations were as 1:2, the expected ratio between the changes in the two cells would be $\frac{12.5 \times 2}{5.4} = 4.6$; while the observed ratio was $\frac{1.0}{0.26} = 3.8$.

The agreement was reasonably satisfactory, and it therefore could be assumed that changes in the concentration of the solutions in the upper cells would be nearly proportional to the amount of salt passing through the diaphragm. Two modifications of the method, however, were sufficient to eliminate entirely the errors due to both diffusion and exosmosis. The error due to diffusion of salts from the intercellular substance was eliminated by filling

the cells, when first set up, with half-strength sea water in the upper cell and sea water in the lower. Thirty minutes was ample for the establishment of a steady diffusion gradient through the tissue between the two solutions. The upper solution was then replaced by fresh half-strength sea water, after which regular readings were taken. In order to eliminate the error due to exosmosis from the protoplasm, such as might be occasioned by toxic salts, 3 controls out of each set of 11 to 13 simultaneous experiments had the more dilute solution in both cells. At the end of the experiment the average conductance of the solution in the upper cells of the controls was taken as a standard of measurement, the average conductance of all the other upper solutions being divided by this figure in order to obtain the percentage which expresses their gain as compared with the control. The figures which were obtained in this manner measure the amount of salt which has passed through the tissue, while the errors due to exosmosis from the protoplasm as well as those due to diffusion from the intercellular substance are eliminated.

5. We must eliminate the error due to variations in the thickness and maturity of the disks of tissue from different fronds, and also that due to variations in the area of tissue through which salt can pass (such as might be introduced by unavoidable smearing of the cement over the surface of the disks).[4] In order to eliminate all of these errors, controls were established in the following manner. After a preliminary half-hour with half sea water in the upper and sea water in the lower cell, the upper solution was replaced with 5.4 cc. of fresh half sea water, and the rate of change of conductivity determined at the end of 2 hours. Both upper and lower solutions were now replaced with solutions of the salt to be investigated (the fresh solutions having the same conductivity as those which they replaced), and the rate of change of conductivity determined after a further period of 2 hours. By dividing the

[4] A single experiment was conducte d to determine the influence of frond thickness. The results were entirely negative. This is in accord with the results secured by ABEL (ABEL, J. J., ROWNTREE, L. G., and LURNER, B. B., On the removal of diffusible substances from the circulating blood of living animals by dialysis. Jour. Pharm. and Exp. Ther. 5: 275. 1914.), who found that diffusion of electrolytes through a collodion membrane was independent of the thickness of the membrane.

figure obtained for the salt in question by that for the control period of the same disks of tissue, we obtain a figure (given in the ratio column of table II) from which all errors due to individual variations of the disks of tissue are eliminated.

6. The method for the determination of the conductance of the solutions was as follows. The solution was poured from the cell into a U tube of such dimensions as to give a conductance of the order of magnitude most accurately determinable, namely, about 1500–2000 ohms$\times 10^{-7}$. The U tube was nearly immersed in a constantly stirred water bath whose temperature, determined to 0°.05 C., varied less than 0°.8 C. in any one set of readings. A temperature correction of 2 per cent per degree Centigrade was applied to the actual readings to reduce them to the average temperature of the set, and the results calculated from the corrected readings thus obtained. A slide wire bridge, a standard 1000-ohm bifilar resistance (supplied with current from the secondary of a Nernst string inductorium at about 300–500 oscillations per second), and a telephone as the zero instrument were used in the customary manner to measure the resistance between bright platinum electrodes immersed in the solution at the opposite ends of the U tube. The distance between the electrodes was fixed. The readings had an error less than ± 0.1 per cent. The check experiments in half-strength sea water usually gave an agreement of corrected readings within ± 0.05 per cent. It will be seen that this degree of accuracy was ample for the purpose.

Results

It is desirable first to find out how fast the various salts pass through the intercellular substance, and whether there is any selective permeability due to any source other than the protoplasm. The data presented in table I show that the cell walls intercellular substance of *Laminaria* are permeable to the salts used, and that the passage through the walls is nearly independent of the nature of the diffusing salt. In dead material the change of concentration is so rapid that owing to the decrease in the concentration gradient the rate of passage of salts through the tissue decreased, as is shown by the lower rate for the longer periods in both sea water and sodium

chloride. It is necessary, therefore, to draw our conclusions from the results of periods of equal length only. The relative permeability to different salts will then be represented by the following figures: calcium chloride 2.2, sea water 2.2, lanthanum nitrate 2.1, sodium chloride 2.1.

TABLE I

PERMEABILITY OF DEAD TISSUE OF *Laminaria*

Solution in upper cell	Solution in lower cell	Duration in hours	Change of conductivity, percentage per hour
Half sea water...	Sea water.....	5.5	1.8
$CaCl_2$, 0.14 M...	$CaCl_2$, 0.28 M..	4.5	2.2
Half sea water...	Sea water.....	12	1.3
" " " ...	" "	5.5	2.2
NaCl, 0.26 M...	NaCl, 0.52 M ..	5	2.0
Half sea water...	Sea water.....	12	1.2
La_2Cl_6, 0.05 M..	La_2Cl_6, 0.10 M..	4.5	2.1
NaCl, 0.26 M...	NaCl, 0.52 M ..	4.5	2.1

It appears probable that the slightly lower rate of diffusion of sodium chloride may have been due to a slight irreversible decrease in the permeability of the intercellular substance caused by the lanthanum nitrate, by which the tissue had been bathed immediately previous to the experiment with sodium chloride. This would be in accord with unpublished data secured by OSTERHOUT by determination of the conductivity of the tissue.

The differences which might be expected to arise as an expression of the diffusion coefficients of the salts are evidently of so small an order as to fail to influence appreciably the rate of diffusion through dead tissue. In view of the very imperfect state of our knowledge of diffusion coefficients, it would be unprofitable at the present time to attempt any further explanation of the influence of that factor in our experiments.

It will be seen from the data given in table II that the presence of living protoplasm greatly decreases the permeability of the tissue as a whole. Living protoplasm offers, therefore, a very considerable resistance to the passage of salts. That it is not normally (in sea water) impermeable to salts will appear from the following considerations. The permeability of the protoplasm for conven-

ience may be considered as the amount of salt passing through the tissue, expressed as the percentage of the amount passing through tissue bathed by sea water, as shown in the ratio column of table II. If the protoplasm be assumed to be wholly impermeable to salts of lanthanum, the figure 0.45, expressing the permeability of the tissue as a whole, would in this case represent diffusion through the intercellular substance only. Since this part of the tissue has been shown (cf. table I) to have no appreciable selective permeability, we may assume that not more than 0.45 of the permeability of the tissues to sea water, which is 1.07, is due to passage of salts

TABLE II

PERMEABILITY OF LIVING *Laminaria*

EXPERIMENT NUMBER	FIRST PERIOD				SECOND PERIOD				RATIO
	Upper solution	Lower solution	Duration h. m.	Change of conductivity, percentage per hour	Upper solution	Lower solution	Duration h. m.	Change of conductivity, percentage per hour	Second period / First period
18..	Half sea water	Sea water	2:05	0.73	Half sea water	Sea water	2:00	0.78	1.07
19..	"	"	2:00	0.79	NaCl, 0.26 M	NaCl, 0.52 M	2:00	1.11	1.41
22..	"	"	2:06	0.73	$CaCl_2$, 0.14 M	$CaCl_2$, 0.28 M	2:02	0.51	0.70
17a.	"	"	1:35	0.73	$La_2(NO_3)_6$, 0.05 M	$La_2(NO_3)_6$, 0.10 M	1:35	0.33	0.45

through the intercellular substance. There remains $1.07-0.45=0.62$, which represents that part of the salt which passes through the protoplasm. In sea water, therefore, a minimum of $\frac{0.62}{1.07}$, or 58 per cent of the salt, passes through the protoplasm, but the exact significance of this figure is doubtful owing to the arrangement of the protoplasmic masses in the tissue.

In order to show the order of magnitude of the total diffusion through the living tissue, the results may be expressed in terms of the amount of salt in gm. molecules passing through 1 sq. cm. of tissue per hour. Ignoring the exceedingly slight change in molecular conductivity induced by such small changes of concentration,

the conductivity will be proportional to the concentration, and a change of 1 per cent in the conductivity of a 0.26 M solution may be assumed to indicate an increase of 0.0026 M in the concentration. An increase of this size in 5.4 cc. of solution will necessitate the addition of $\frac{5.4}{1000} \times 0.0026$, or 0.0000140 gm. molecules of salt. If we divide the figures obtained in this manner for the various salts, by the area of tissue in sq. cm. through which salts can pass, we obtain the figures given in table III. The figure for sea water was obtained by assuming all of its conductivity to be due to sodium chloride; but since sea water contains about 12 per cent of its electrolyte as salts of bivalent elements, which have a higher molecular conductivity than sodium salts, its actual molecular content is less than that of a sodium chloride solution having the same conductivity, and the figure given in table III is thus slightly too high.

TABLE III

GRAM MOLS DIFFUSING PER SQ. CM. PER HOUR THROUGH LIVING *Laminaria*

Upper solution	Lower solution	Gm. mols diffusion
Half sea water.....	Sea water.....	0.0000425
NaCl, 0.26 M.....	NaCl, 0.52 M.....	0.0000610
$CaCl_2$, 0.14 M.....	$CaCl_2$, 0.28 M.....	0.0000150
$La_2(NO_3)_6$, 0.05 M..	$La_2(NO_3)_6$, 0.10 M...	0.0000034

The data of tables II and III also show that there is a selective permeability to the salts used. Sodium chloride is allowed to pass through the tissue most rapidly, the salts of sea water next, calcium chloride considerably less rapidly than sea water, and lanthanum nitrate least of all. That the effect is produced in large part by the kations, as was to be expected, is shown by the fact that preliminary experiments with lanthanum chloride (lacking the preliminary comparison period in sea water) showed a permeability comparable with that to lanthanum nitrate. Thus in one experiment with lanthanum chloride the change of conductivity of the upper solution was 0.30 per cent per hour, while that quoted for lanthanum nitrate is 0.33 per cent per hour. Whether

protoplasm is at all permeable to lanthanum salts cannot be decided with the data furnished by these experiments.

It might be supposed that the protoplasm was normally more permeable to sodium chloride than to the other salts of sea water, and that therefore when bathed by pure sodium chloride solution more salt would pass through the diaphragm. On the assumption that the tissue is permeable only to the sodium and potassium chlorides, the molecules of which constitute 88 per cent of the molecules of salt in sea water, the rise in permeability on substitution of sodium chloride solutions for sea water would be only that from 88 to 100. The observed rise is much greater, namely, from 76 to 100, and in addition it must be remembered that the calcium and magnesium salts of sea water are probably able to penetrate the tissue to some extent. Sodium chloride must increase the permeability of the tissue therefore.

By analogy, it might be assumed that the permeability of the protoplasm decreased under the influence of calcium and lanthanum salts. In order to obtain more exact information in respect to this question, a set of experiments was conducted in which the permeability was determined during successive periods of treatment with a given salt. The solutions in both the upper and lower cells were renewed at the beginning of each period. The results are shown in table IV and fig. 2.

From these experiments it will be seen that the increase of permeability due to sodium chloride is progressive, and that it leads in the course of about 4 hours to a permeability of the tissues corresponding to that of dead material. The effect of calcium chloride, on the other hand, is to cause a temporary decrease in permeability, followed by a rise which at the end of about 12 hours leads to a permeability comparable with that for dead material. At the end of this time the material had assumed the green color characteristic of dead material.

The experiment with sea water was conducted under conditions extremely unfavorable to the maintenance of normal permeability, the temperature rising to 14° C. during the third and fourth periods. Partial recovery is shown in the succeeding periods during which the temperature decreased. The last period was begun about 24

hours after the beginning of the experiment, and shows that the tissue, which had only partially recovered its normal permeability,

TABLE IV

PROGRESSIVE CHANGES IN PERMEABILITY OF TISSUE OF LIVING *Laminaria;* EXPRESSED AS RATE OF CHANGE OF CONDUCTIVITY OF SOLUTION IN UPPER CELL, IN PERCENTAGE PER HOUR

UPPER SOLUTION, HALF SEA WATER; LOWER SOLUTION, SEA WATER			UPPER SOLUTION, NaCl, 0.26 M; LOWER SOLUTION, NaCl, 0.52 M			UPPER SOLUTION, $CaCl_2$, 0.14 M; LOWER SOLUTION, $CaCl_2$, 0.28 M		
Period begun at	Duration in min.	Rate of change	Period begun at	Duration in min.	Rate of change	Period begun at	Duration in min.	Rate of change
6:45 A.M..	120	0.67	2:40 P.M....	120	1.11	9:33 A.M....	122	0.51
9:15 A.M..	124	0.78	5:10 P.M ...	150	2.30	12:05 P.M....	124	0.82
11:45 A.M..	121	1.01	8:15 P.M....	130	2.50	2:45 P.M....	121	0.69
2:20 P.M..	132	1.27	.....	.....	.....	5:25 P.M....	120	1.37
5:00 P.M..	170	0.81	.....	.....	.....	8:10 P.M....	135	2.05
8:20 P.M..	139	0.97	.....	.....	.....	.....	.....	.....
6:05 A.M..	120	0.96	.....	.....	.....	.....	.....	.....

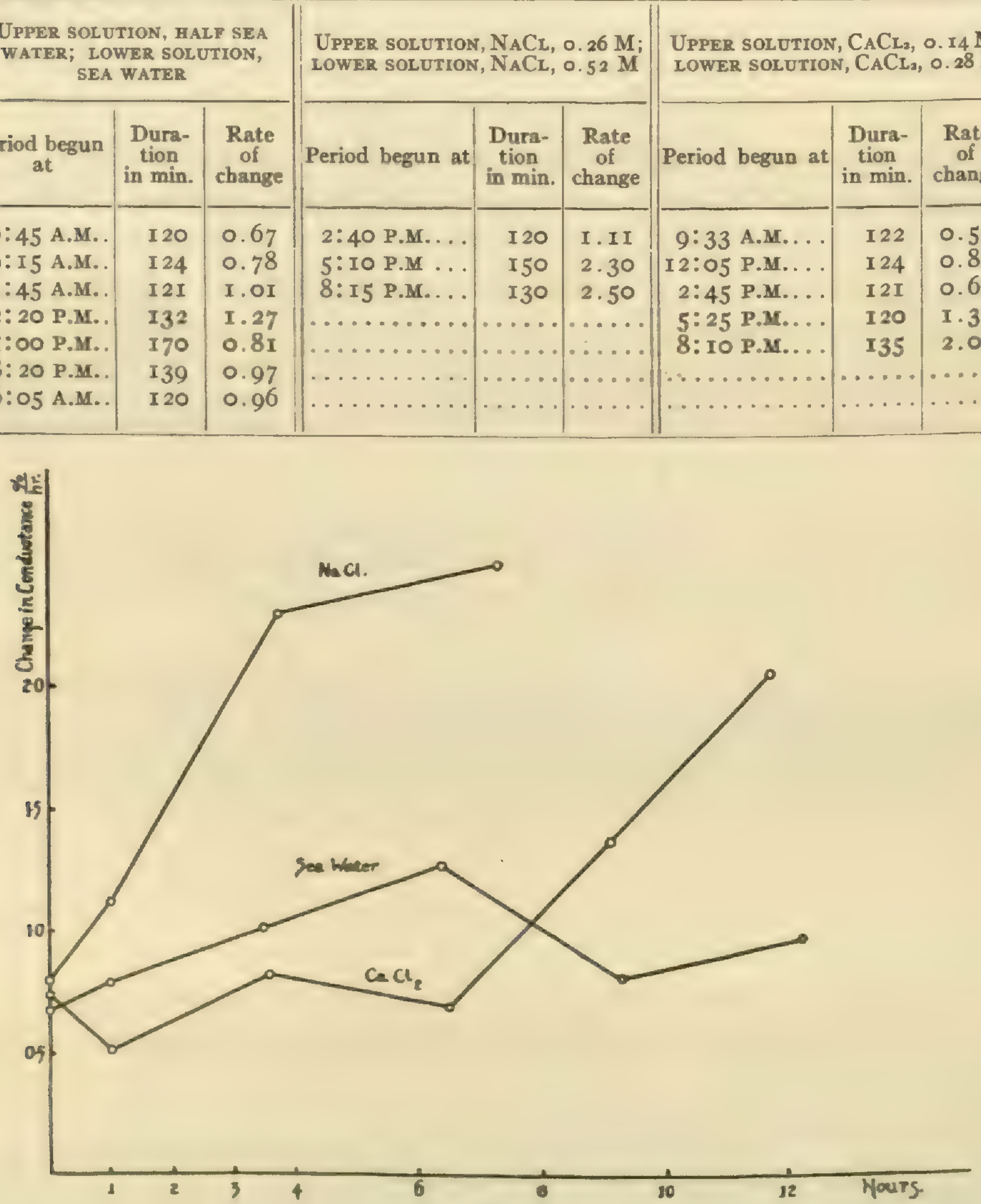

FIG. 2

suffered no further injury during the period of low temperature (0–4° C.) intervening between the fifteenth and twenty-fourth

hours. The disks were still brown and apparently uninjured even after 48 hours in the apparatus. Certain experiments with lanthanum salts indicated that the effect of lanthanum would resemble that of calcium, differing chiefly in that the alterations of permeability would take place more rapidly.

Summary

1. The protoplasm of *Laminaria* is normally permeable to the salts of sea water.

2. Sodium salts cause an increase of permeability which culminates in death.

3. Calcium and lanthanum salts cause a decrease in permeability, followed by an increase which culminates in death.

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EVAPORATION RECORDS FROM THE GULF COAST

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(WITH FOUR FIGURES)

In connection with field work in northern Florida, undertaken to determine the composition and limits of certain gulf coast forest associations and their relations in succession, and following the instructions of LIVINGSTON,[1] FULLER,[2] and the work of others in the north and west, records of the daily rate of evaporation in several of the typical plant associations were kept, some of them running through a period of 19 successive months. The Livingston rain-correcting atmometers were used and care was taken to follow the directions for their operation in all particulars. It was planned to visit each station once in two weeks, and this was carried out with few interruptions.

Station no. 1 was in an upland hammock forest on Norfolk Fine Sandy Loam. *Magnolia grandiflora*, *Fagus grandifolia caroliniana*, and *Acer floridanum* Pax (or *Acer saccharum floridanum* Sarg. Silva N. Am.) were the chief trees, with an undisturbed growth of young trees of these and other species and of mesophytic shrubs and herbs. The apparatus at this station suffered various mishaps, and the record is broken, but from January to May 1913, which includes the times of extreme minimum to maximum evaporation for all the stations (except that of *Pinus palustris*), the record is complete.

Station no. 2 was in an upland oak forest on Orangeburg Fine Sandy Loam, 2.5 miles west of Tallahassee. In this forest nine-tenths of the trees were deciduous, with *Quercus falcata*, *Q. stellata*, and *Carya alba* predominating. *Cornus florida* was common, but *Q. virginiana* and *Ilex opaca* (broad-leaved evergreens) were rare. *Myrica cerifera*, *Rhus copallina*, *Ilex vomitoria*, *Ceanothus americanus*, *Aralia spinosa*, *Vaccinium stamineum*, *Callicarpa americana*,

[1] LIVINGSTON, B. E., Evaporation and plant habitats. Plant World **11**:1–9. 1908; Operation of the porous cup atmometer. Plant World **13**:111–119. 1910.

[2] FULLER, G. D., Evaporation and plant succession. BOT. GAZ. **52**:193–208. 1911.

and *Viburnum rufidulum* were the principal shrubs about the station and made a rather close shrubbery throughout the woods. The list of herbs shows nothing especially distinctive in the way of species, as they are practically the same as those of the beech and short-leaved pine forests in which stations 3 and 4 were located.

Station no. 3 was in an upland short-leaved pine forest about 1 mile north of Tallahassee, on Orangeburg Sand. The mature trees were almost entirely *Pinus echinata*, but this wood was well advanced in the undergrowth toward the oak-hickory stage; the young half-grown trees of *Quercus falcata*, *Q. stellata*, and *Carya alba*, and also of *Q. virginiana* and some *Fagus grandifolia caroliniana*, made one story, under which was a lower growth of *Quercus nigra*, *Q. laurifolia*, *Q. marilandica*, *Crataegus* spp., *Prunus angustifolia*, *Cornus florida*, *Nyssa sylvatica*, *Vaccinium arboreum*, *Callicarpa americana*, and *Viburnum rufidulum*, with numerous lianas as *Smilax glauca*, *S. pseudo-china*, *Cissus* spp., *Vitis rotundifolia*, *Gelsemium sempervirens*, and *Lonicera sempervirens*. Common herbs of the station vicinity were *Arisaema Dracontium*, *Oenothera biennis*, *Sanicula canadensis*, *Gerardia purpurea*, *Mitchella repens*, *Eupatorium album*, and *Chrysopsis mariana*.

Stations 2 and 3 were operated for 19 months continuously without a break or mishap.

Station no. 4 was in a beech wood about one-fourth of a mile east of the station in the pine forest. To the west and south of this forest was a short-leaved pine wood in a still later stage than the one in which station 3 was placed. The proportion of deciduous trees was larger and the trees older, while the undergrowth was much less dense, which may largely be accounted for by the fact that this wood had been stocked with hogs and cattle for some years. To the north its character changed quite abruptly, the pines being few and the number of mature deciduous trees not large, but the undergrowth was very dense. Throughout this wood (an area of some 40 acres) were scattered beeches of all ages. Magnolias were less common. The beech opening in which the station was located apparently had once been somewhat swampy, although but little lower than the rest of the ground and scarcely wetter except after heavy rainfalls. As a whole the forest was level and formed part of

a level hilltop. The soil was mainly Orangeburg Sand, which is a transitional type between the Orangeburg and Norfolk Fine Sandy Loams, and which, as stated in the soil survey, is occasionally found in small isolated patches within the Orangeburg Loam areas, occupying slight elevations which have not suffered from erosion.

The evaporimeter was placed in the portion of the woods freest from shrubs or undergrowth of any kind, there being comparatively few herbs in the vicinity, those noted being mainly the same as those of the open pine wood, except that the fireweed (*Erechtites hieracifolia*) was common. This station suffered several interruptions during the 18 months of its operation, owing to the pasturing animals and other causes.

The four stations described were all on the hills or elevations over 100 ft. above sea level, and none of them suffered from frost.

Station no. 5 was established in September 1912, about 5 miles southwest of Tallahassee, on low sandhill soil, a strip of gently rolling yellowish sand, covered with a dense growth of scrub oaks, only an insignificant part being under cultivation. It has doubtless been a shoal, extending east and west parallel with the edges of the abrupt upland to the north which once formed the shore line. This sandhill area is characterized everywhere by a very definite as well as limited tree flora. There are 3 scrub oaks and 2 pines, the latter being scattered. *Quercus catesbaea*, *Q. margaretta*, *Q. cinerea*, and the long-leaved pines, *Pinus palustris* and *P. caribaea*, are the species. The chief undershrubs near the station were *Asimina pygmaea*, *Vaccinium arboreum*, and *V. corymbosum*. *Ascyrum hypericoides* was also noted at this station and appears to be generally ubiquitous, although frequent rather than abundant. The herbs were *Asclepias tuberosa*, *Scutellaria integrifolia*, *Gerardia purpurea*, *Eupatorium aromaticum*, and *Liatris laevigatus*. Although the sandhill region is very sparsely inhabited, the records from this station happened to be frequently interrupted by meddlesome hunters as well as by fire, frost, and a cyclone. In the effort to keep the apparatus hidden it was twice moved. The cup was broken by frost on November 28, 1913.

Station no. 6 was in a long-leaved pine forest on Norfolk Sand, 4 miles southwest of Tallahassee and a quarter of a mile north of

station no 4. At this station the evaporimeter was broken by frost once in the second winter of its history, on January 11; it was shot to pieces once; and was once in the immediate path of a June cyclone which blew down most of the trees in a track 800 ft. wide. By this storm the cup was demolished but the reservoir was unbroken. The location was then changed a few rods to the east. This station was peculiar in that the trees were essentially like those of the Leon Sand station (no. 7) near Lake Jackson, and the herbaceous plants like those on the sandhill soil. At the outer border of this soil, where the Norfolk Sand and the sandhill join, the scrub oaks gave way abruptly, the line between the two soils being generally as sharp as if the planting had been artificial.

The Leon Sand station, no. 7, was in operation more or less continuously for 18 months, being broken by frost once the first winter and twice during the second winter; it was also once in the path of a fire. This Leon Sand is situated 9 miles northwest of Tallahassee, being a strip of long-leaved pine forest about 200 yards wide. This small area is bordered on the north by a slough which is directly bordered by Norfolk Sand, and to the south the soil is the Norfolk Fine Sand, each with characteristic vegetation. This strip of the Leon Sand is an outlying neck of a larger area of the same soil 2.5 miles wide and 1 mile long, the only area of this particular soil in the northern part of the county which is accessible to the railroad. However, in its growth it is typical of the larger area of the flatwoods to the southeast. This soil, wherever it occurs, is very level and poorly drained and therefore excessively wet a large part of the year. Station no. 7, therefore, was on the wettest soil of any, and its vegetation should be compared with that of station no. 6, which also supported a long-leaved pine forest on the Norfolk Sand, one of the driest soils of the region. The wood on the Leon Sand was very open and the destruction caused by turpentining had still further thinned it. Owing partly to frequent fires and partly to the general quality of the soil and the drainage, the undershrubs were very low, seldom exceeding 2 ft. in height. The forest floor was sparsely covered with wire grasses. Apart from the pines, the trees noted about this station were occasional small specimens of deciduous trees, as *Quercus falcata*, *Q. virginiana*, *Q.*

nigra, *Liquidamber styraciflua*, *Acer rubrum tridens*, and *Nyssa sylvatica biflora*. The undershrubs were *Quercus myrtifolia*, *Q. minima*, *Pyrus arbutifolia*, *Rubus villosus*, *Rhus copallina*, *Ilex glabra*, *I. lucida*, *Hypericum fasciculatum*, *Vaccinium virgatum tenellum*, *Viburnum nudum*, and *V. molle*. A common liana was *Gelsemium sempervirens*, but the most common plant of all was *Serenoa serrulata* (saw palmetto). The herbs about this station make a distinctive list, the majority being species of Compositae, as *Helianthus angustifolius*, *Rudbeckia laciniata*, *Aster Tradescanti*, *Solidago fistulosa*, and *Bidens bipinnata;* there were also *Polygala lutea*, *Viola lanceolata*, *Sabatia gracilis*, *S. lanceolata*, *Pinguicula lutea*, and *Valerianella radiata*.

Stations no. 8 and no. 9 were located in October 1913 in the meadow of the Ocklocknee River. One was placed in a willow growth on the south bank, the apparatus being located in the outer border of the narrow strip of trees edging the stream and 5 or 6 ft. above the water at its normal stages. At this point a strip of bare sand, 15–20 ft. wide, separated the willows from a birch zone. Immediately bordering the river this meadow strip was about one-fifth of a mile wide, bounded on the east by a strip of Norfolk Sand with the long-leaved pines. The area occupied by the willows was subject to frequent overflow and no other plants seemed able to maintain themselves permanently in this zone. The growth here was not luxuriant, few of the trees exceeding a height of 10 or 12 ft. The records from these stations were interrupted by frost about December 21, 1913, and again on January 18, 1914, while from February 1 to March 28 the apparatus was covered by water two-thirds of the time and no records were secured. The birch station, 4 ft. higher and 15–20 ft. farther inland than the willow station, suffered similar interruption, except that the interval due to the flood was two weeks shorter and the apparatus was reestablished March 15, at which time the willow station was still completely under water. On the whole, the growth here was more luxuriant, although few of the trees had trunk diameters greater than 6 inches, or height greater than 15–20 ft.

Laboratory examination of each of the soils at the several stations was made to determine the organic content and general

character. The Orangeburg Fine Sandy Loam soil from the Spanish oak-post oak station, when dried, was a dark brownish gray. It is an excellent soil, rich in humus, and the drainage in the locality of the station was good. The soil from the short-leaved pine station was a medium brownish gray, similar to the preceding but containing a larger proportion of sand (Orangeburg Sand), and less humus. The soil from the beech wood was the same according to the classification of the United States Soil Survey Report, and it resembled that of the pine wood in the samples taken in the course of this study, but both soil and subsoil were of a brighter reddish tinge. The area of the beech station was hardly so well drained as that of the pine wood. The soil from the *Pinus palustris* forest on Norfolk Sand was very similar in color (both soil and subsoil) to that of the short-leaved pine, but contained decidedly less clay, separating in loose grains when dry, while the other dried in small lumps. It was also less rich in humus. The drainage was excellent to excessive. The soil from the scrub oak forest (which adjoined the preceding on the south) was very similar to Norfolk Sand in texture but a brighter red and perceptibly poorer in humus. The soil from the Leon Sand station was a medium gray sand with a very small admixture of organic materials. It was too wet for agricultural crops.

The evaporation records from the mesophytic forest (station no. 1), during the time it was steadily running, showed a consistently lower average and actual rate than any other station. The minimum monthly rate for this station was 6.05 cc. per day in January. The actual minimum was 4.5 cc. in January. The maximum monthly rate was 10.27 cc. daily in April, and the actual maximum was 11.9 cc. the first of May. The mean average rate for the 4 months covering the time from the minimum to the maximum was 8.5 cc. per day, an interesting result in comparison with the record of evaporation for beech-maple forests in the north.

Station no. 2, the Spanish oak-post oak forest, in comparison, gave a record of 9.90 cc. per day for the same period of the same year. The average of this station for 18 months' continuous and unbroken record, however, is 14 cc. daily. The minimum monthly

average is 9.94 cc. per day in December, and the maximum monthly average is 22.20 cc. daily in April. The actual minimum during the 18 months was 7.01 cc. in October, and the actual maximum was 29.28 cc. in March.

The short-leaved pine station, no. 3, averaged 11.67 cc. per day for the same period of the same year as given for stations nos. 1 and 2; and for an 18 months' unbroken record, 14.22 cc. per day. The minimum monthly average was 8.83 cc. per day in January, and the maximum monthly rate 19.7 cc. daily in April. The actual minimum was 5.18 cc. in January, and the actual maximum was 25.04 cc. in May. Comparison of stations 2 and 3 thus shows the averages as based on the yearly rate to be very similar. If, however, a comparison be made of their rates during the two general periods for deciduous trees, namely, with full foliage and without full foliage, or summer and winter (from June to November, and from November to June), the comparison shows that the June to November season gave a rate of 12.49 cc. daily for the oak forest, and of 13.8 cc. daily for the pine forest; while the winter rates (November to June) were, respectively, 15.69 cc. and 13.70 cc. This demonstrates a greater evaporation in winter in the deciduous forest, and the greater evaporation in summer from the pine forest. However, the similarity in the yearly rate, covering as it does the extremes of the two years, shows that the evaporation in the two forests was not greatly different, and this may seem related to the fact that at both stations there was an abundance of shrubbery of similar composition; if anything, that of the pine wood, being in two stories, was the thicker, and the telescoping of these two associations was conspicuous.

The beech forest, which had been burned and pastured, gave an average result of 16.63 cc. daily for the whole period of 18 months (with one break in the record for November to December 1912), an average of 11.21 cc. per day for the period from January 1 to May 1, 1913, and an average of 13.4 cc. for the summer (full foliage) period. This last compares with the same average of the pine wood, showing a similarity between the pine forest and the pastured beech wood. June shows the minimum monthly rate for this forest, and March the maximum (fig. 1).

Station no. 5, that of the scrub oaks, gave 15.52 cc. daily for 18 months, and 15.30 cc. daily for the period from January to May 1913. For the summer (June to November) the average was 13.95 cc. daily, corresponding to the short-leaved pine and the pastured beech wood. The winter rate was 14.1 cc., intermediate between that of the oaks and pine. The period of greatest evaporation was April; while December, January, and February showed

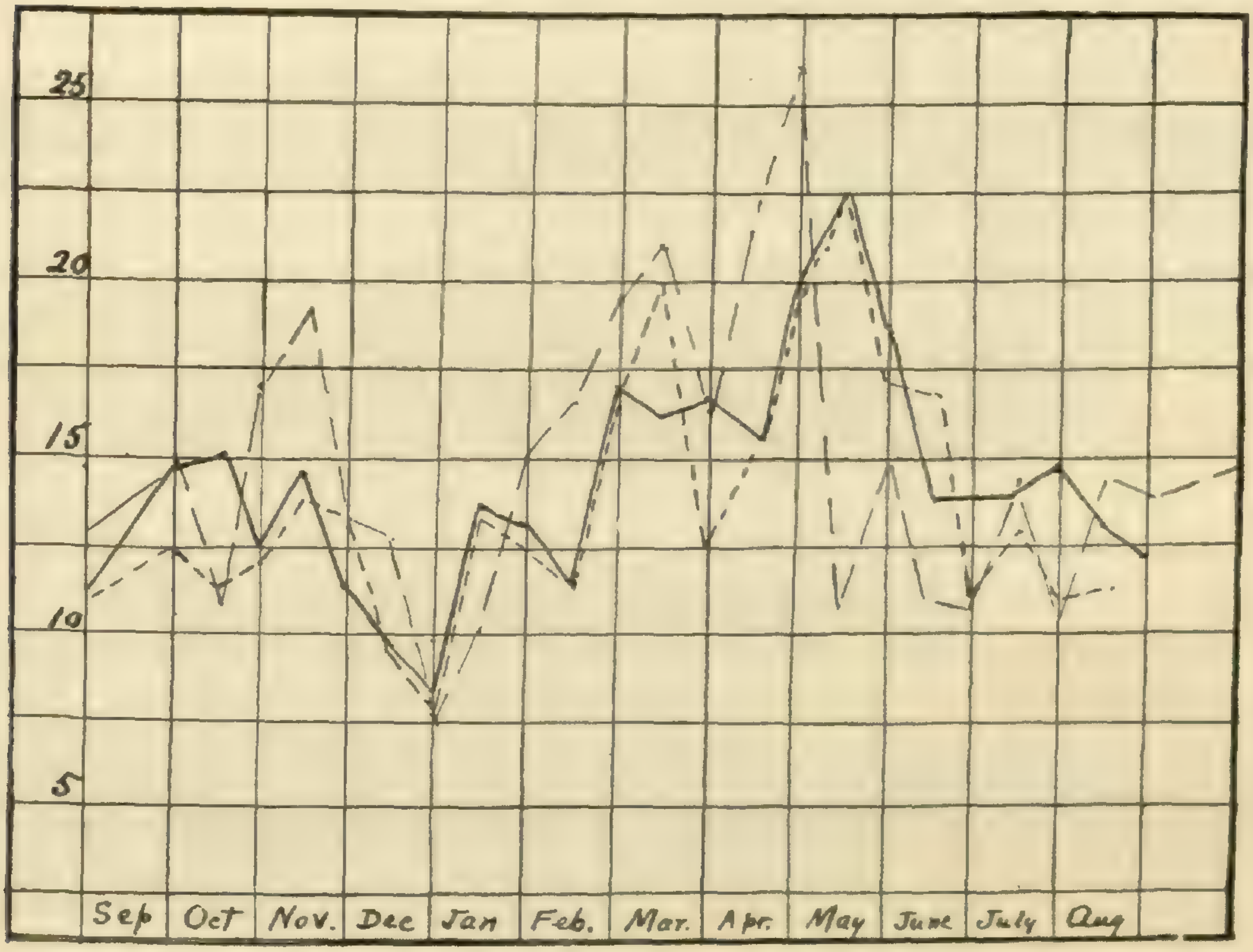

FIG. 1.—Chart showing comparison of yearly range of evaporation in Spanish oak-post oak forest (dotted line); short-leaved pine forest (heavy line); grazed beech forest (broken line).

about the same minimum. The actual minimum was 7.39 cc. in late December, and the actual maximum 27.97 cc. in early May. This forest, therefore, does not show such wide variation for the seasons as do the others given, and the curve representing the years' averages runs more evenly for this forest than does that of any other except the flatwoods. This evenness may be related to the fact that, although the trees are deciduous, their leaves, after dying and turning brown, remain on the branches most of

the winter; and as they are coriaceous in texture and more or less coated with felt on the under surface, they remain intact until the time for the new foliage. The low summer rate (as compared, for example, with the long-leaved pine rate) also may have a relation to the fact that although there is an absence of shrubs or undergrowth of importance, these trees are dwarfed or scrub-like, and the foliage grows low on the trunks; when growing closely they make a thicket-like forest.

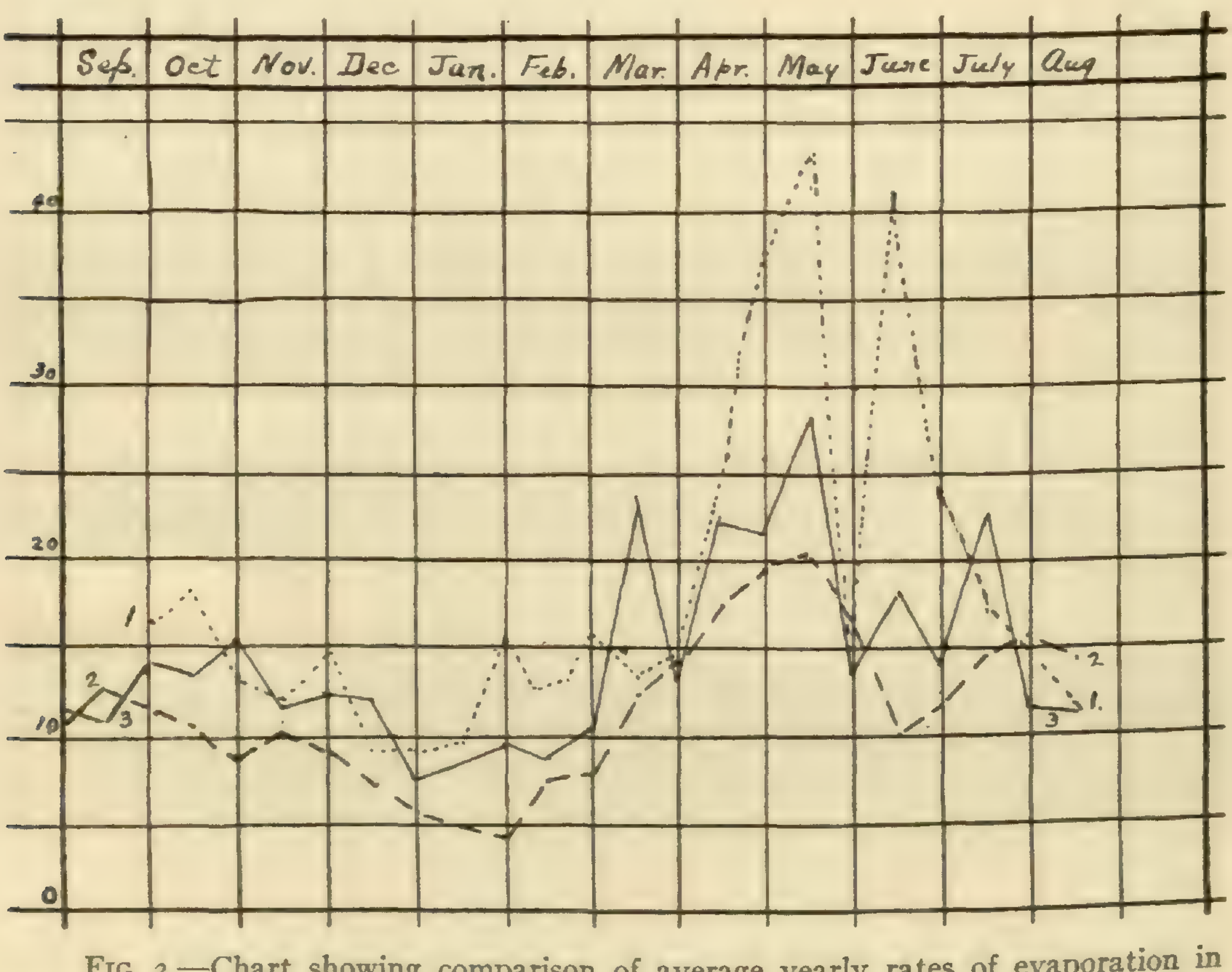

FIG. 2.—Chart showing comparison of average yearly rates of evaporation in scrub oak forest (heavy line); flatwoods (broken line); long-leaved pines on dry land (dotted line).

Station no. 6, in the dry pine wood, gave the average evaporation per day of 17.9 cc.; 12.28 cc. for the period January to May; 18.25 cc. for the summer period; 19.2 cc. for the winter period; with minimum monthly average of 8.9 cc. in December and a maximum of 32.5 cc. in April. The actual minimum was 4.15 cc. and the maximum 56.19 cc., showing the widest range of any station (fig. 2).

The flatwoods station, on Leon Sand, gave an average for 18 months (with a break in the record for December and January 1912–1913) of 12.99 cc. per day. The January to April average for 1913 is not complete, but for the summer and winter periods the averages are, in order, 13.24 cc. and 11.17 cc. The minimum month is January, 5.94 cc. per day; the maximum in May is 19.8 cc. per day. The actual minimum falls lower than that of any other, being 3.88 cc. in February, and the maximum was 25.44 cc. in May.

The meadow stations were not in operation for a long enough time to give results covering a year. From October to June the willows averaged 12.47 cc. daily, comparable to the flatwoods station. The average for the birch station for the time was 13.98 cc. daily. Their minima occurred in January and maxima in May.

Arranging the stations in the order of their yearly averages of evaporation, beginning with that having least evaporation, their order is as follows: hammock climax forest, willow (meadow) zone, flatwoods, birch (meadow) zone, Spanish oak-post oak forest, short-leaved pine forest, scrub oak forest, beech wood (open and grazed), long-leaved pine forest. Omitting the meadow stations, the others arranged in order of increasing rates are (for the summer period June to November), after the hammock forest, the Spanish oak-post oak forest, the flatwoods, the beech (grazed), the short-leaved pines, the scrub oaks, and long-leaved pines. The order, by winter average rates, is flatwoods, short-leaved pines, scrub oaks, Spanish oak-post oak, beech (grazed), and long-leaved pines. The order during the critical period of the year, from January to May (a dry period and a time of sharply rising temperature, corresponding to the time of vernation of the deciduous trees and of changes of leaves, in part or altogether, of many evergreens), is as follows: mesophytic hammock forest, Spanish oak-post oak forest, beech wood (grazed), short-leaved pine wood, long-leaved pine wood, and scrub oaks. Of these the order of the forests on the clayey soils of the upland is essentially that observed for their succession, the difference in winter being in the place of the leafless Spanish oak-post oak forest as compared with the conifer forest. In the pine and oak forests on the dry sandy soils, the same relation

FIG. 3.—Chart showing evaporation rates of 3 pine forests: long-leaved pine on dry sand (heavy line); long-leaved pine on wet sand (broken line); short-leaved pine (light line).

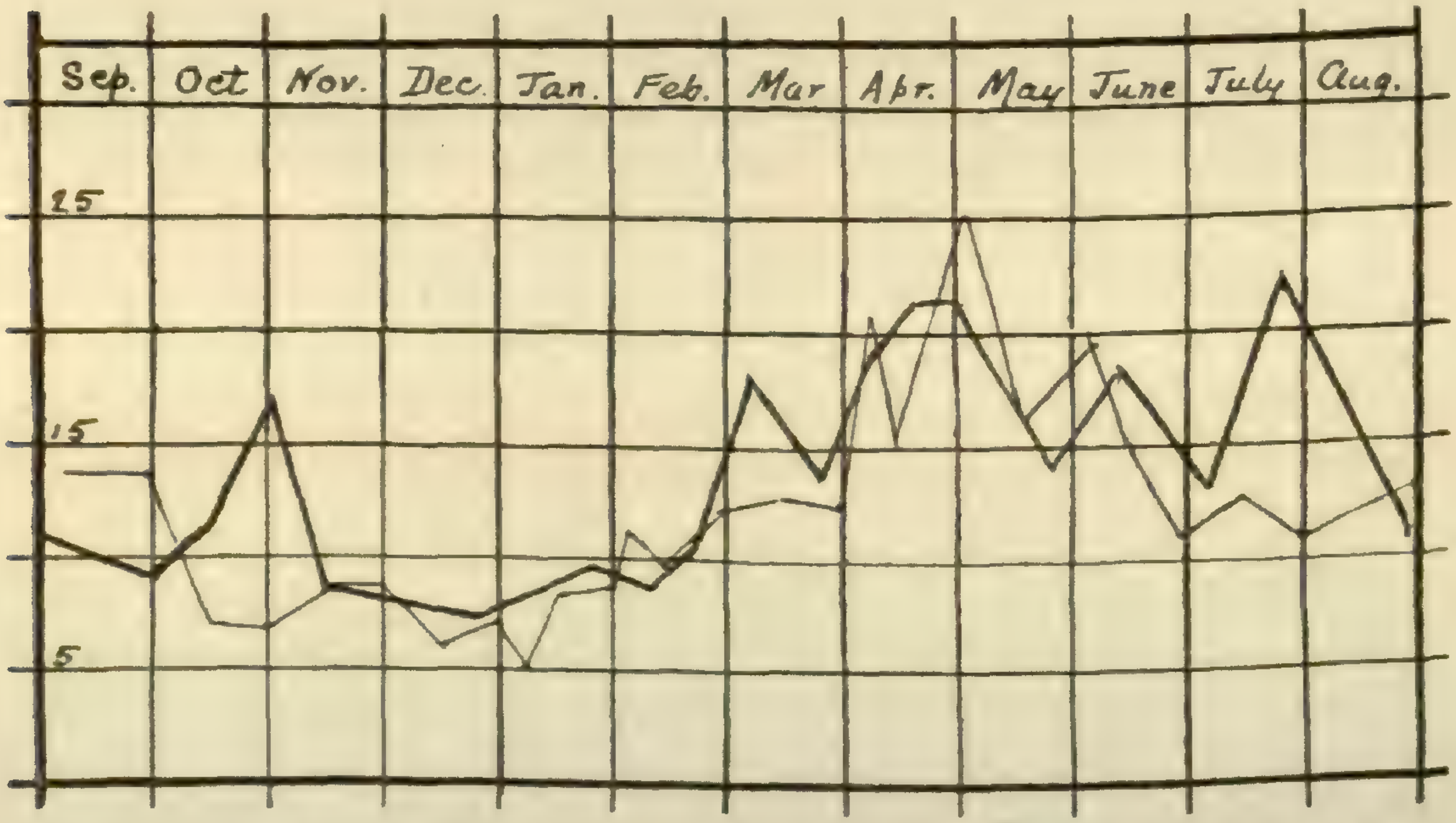

FIG. 4.—Chart showing comparison of evaporation rates, during same year, in the 2 oak forests: scrub oaks (heavy line); Spanish oak-post oak forest (light line).

holds, the oaks showing a higher winter rate than the pines. The two pine forests (short-leaved and long-leaved) on dry soil are nearest together in their evaporation rates during the spring. A comparison of the three pine associations and the two oak associations as charted will show these relations (figs. 3, 4).

The Leon Sand forest is singular in that it is so directly related to the soil moisture, and although all other factors tend to make the evaporation excessive, the constant humidity near the soil surface of the ground, owing to the soil saturation, modifies the curve until it is the most equable of any of those described in this report.

RICHMOND, IND.

FATS FROM RHUS LAURINA AND RHUS DIVERSILOBA[1]

JAMES B. MCNAIR

(WITH ONE FIGURE)

STEVENS (12) has noticed that the green fruit of *Rhus radicans* is very poisonous. STEVENS and WARREN (13), when investigating the fruit of *R. vernix*, found the green fruit highly toxic, while the ripe fruit is harmless. WARREN (15) attributes this interesting change in toxicity to an apparent replacement of acrid resins by wholesome and palatable fats. Besides these species of *Rhus*, a fat (Japan wax) has been found in 4 species of *Rhus: R. succedanea* L., *R. acuminata* DC., *R. vernicifera* DC., and *R. sylvestris* Sieb. and Zucc. (6). All 6 of these species are poisonous, and it is interesting to note that the discovery of fat in the fully matured fruit of *Rhus laurina* Nutt. may add a non-poisonous species to the list.

Investigations were begun by me on the fats from *Rhus laurina* Nutt. and *R. diversiloba* T. and G. with two objects in view: (1) to discover whether or not these fats are identical with Japan wax, and (2) to determine, if possible, the connection between this fat and the poisonous property of *R. diversiloba*. This latter problem appeared all the more interesting when the fact became apparent that during the ripening of the drupes their poisonous properties simultaneously decreased with their increase in fat. When the fruits have reached full maturity (when the semi-transparent epidermis loosens and easily falls off from the waxy mesocarp) they are non-toxic. The toxicity was tested by thoroughly rubbing the pulverized fruits, as well as an alcoholic solution from them (concentrated to one-third of the original volume of the fruits), on the skin of a sensitive person.

The fats experimented with were obtained by boiling the ripe fruits in 95 per cent alcohol under a reflux condenser. The fat samples were purified by repeated solution, evaporation of the

[1] Contribution from the Rudolph Spreckel's Physiological Laboratory of the University of California.

solvent, and crystallization of the solid matter. The substances thus purified are pale yellow, hard, with a conchoidal and somewhat lustrous fracture. Their odor recalls that of tallow and beeswax. Under the microscope they appear to consist of small and large refractive grains. They are insoluble in water, slightly soluble in cold 95 per cent alcohol and ether, easily soluble in hot 95 per cent alcohol (separate on cooling to granular crystalline

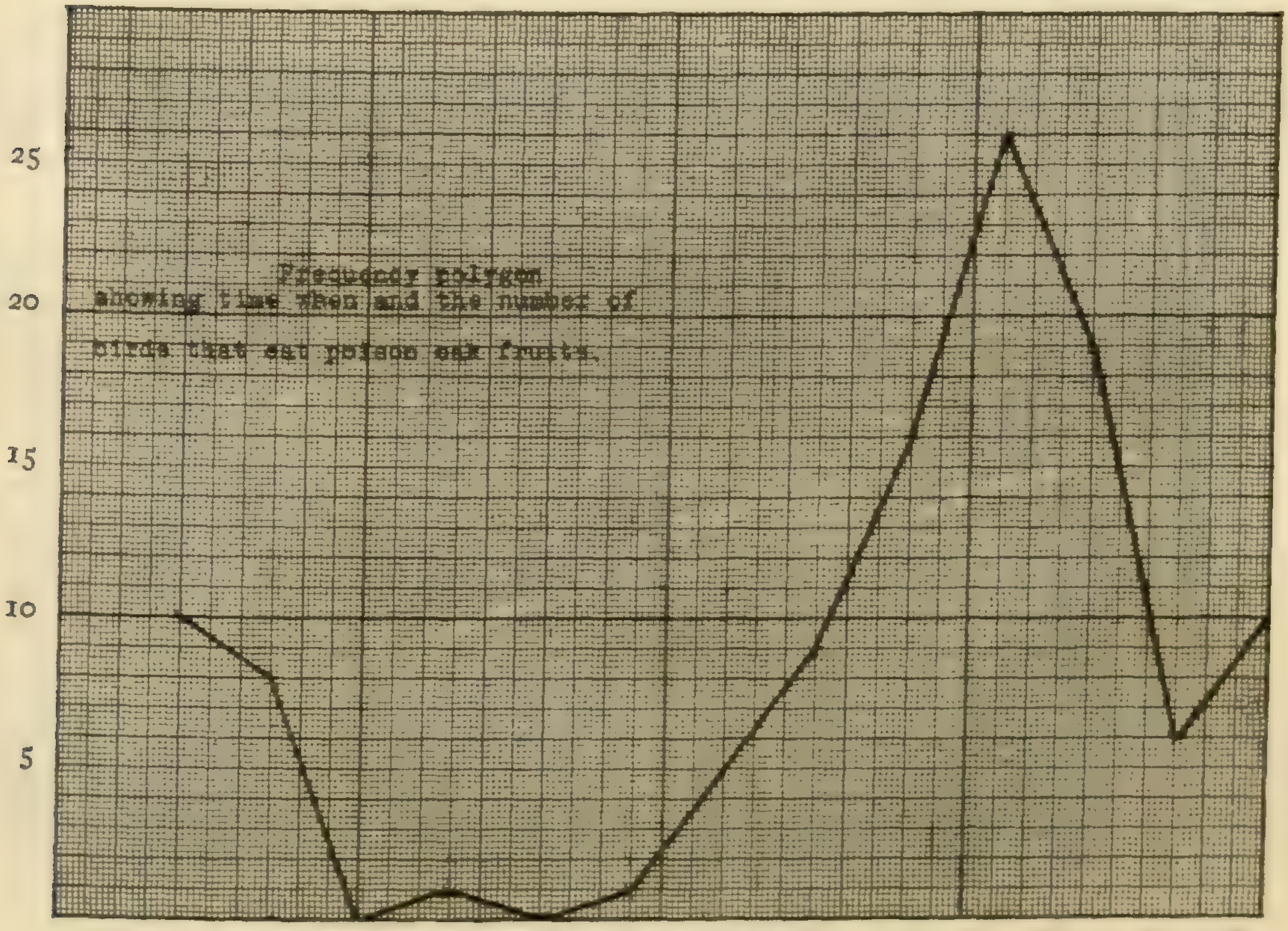

FIG. 1

mass), warm ether, benzol, petroleum ether, and carbon bisulphide. They form grease spots when melted on filter paper. That glycerol is probably a constituent is evident from an irritating odor of acrolein evolved when the substances are mixed with powdered potassium bisulphate and heated in a dry test tube.

From a consideration of their physical and chemical properties so far determined, the fats from *R. laurina* and *R. diversiloba* seem to be similar to Japan wax. This means that similar fats have been found in a non-poisonous and a poisonous species of *Rhus*.

The wide variance in the physical and chemical constants of Japan wax obtained by different experiments, and different experiments by the same investigators, may have been due to several factors, namely, adulterations of water, starch, oil of *Perilla ocimoides* Linn. (BRANNT 2), tallow (BRANNT), the fact that the fat becomes transparent below its fusing point (18–23.5° F. below m.p., BRANNT), the fact that the melting point becomes higher with the age of the sample (BRANNT), impurities, and different methods of analysis.

TABLE I

ANALYTICAL FIGURES OBTAINED

	R. diversiloba	*R. laurina*
Specific gravity...	0.9872 18°.5 C	0.8987 18°.5 C
Solubility*.....	170	136
Iodine absorption.	8.79 per cent (Hübl.)	11.44 per cent (Hübl.)
Saponi value†....	220.6	157.1
Melting point....	53° C.	74° C.

* Mg. per liter in 95 per cent alcohol at 20° C.
† Mg. KOH per gm.

Morphology of fruit of R. diversiloba in relation to fat formation

The ripe fruit of *R. diversiloba* is oval, 5–9 mm. broad, 4–6 mm. high, and 4–6 mm. thick. When first formed it has a shining grass-green color and smooth texture. When dry it becomes brown and presents long dark stripes which previously were only slightly indicated. The outer surface of these stripes is depressed because of the collapsing of the large resin ducts which lie directly beneath them. The outer layer of the fruit, which is a drupe, is something over 1 mm. thick. In the horizontal cross-section 20–30 large resin passages are present. These form a single outer row completely around, which conforms with the general outline of the drupe. Many smaller resin ducts are present, which alternate with the wider ones to form a row next to the seed. The arrangement on the top and bottom of the drupe is less regular. The epidermis is bordered by 2 or 3 layers of strong sclerenchymatous cells. Between these border layers and the resin passages lies the parenchymatous tissue whose cells for the most part contain solid fat. In

the ripe fruit the fat appears in the principal tissue of the mesocarp. Fat is not found in the exocarp, the thin walls and the inner boundary of the mesocarp, the sclerenchymatous cells, the cells of the vascular bundles and their sheaths, and the parenchymatous sheaths of the resin passages.

The presence of solid fat in the fruit cannot be detected before July. At the beginning of August fat formation is nearly completed. The granulated layer of fat can be seen in the cell between the membrane and the protoplasm. This layer makes the lumen smaller, increases on the outside, and goes in between the already formed fat. Its granular form changes to striated masses. Before the formation of this fat in the fruit a progressive increase in the starch content is noticeable. Starch forms partly in the chromatophores in the cell and partly in the cells. When the fruit cells are rich in starch the cells contain besides only granular protoplasm and nuclei. This starch gives a positive reaction with iodine. When fat formation is near completion no starch can be detected in the fruit. In fruits which have nearly completed their growth the resin passages are everywhere constricted by the growth of parenchyma sheaths. From a consideration of these phenomena fat is apparently formed from starch and not from the resin-like poisonous sap.

This view does not seem untenable, for it has been proved that in the storage foods of plants carbohydrates and fats are interchangeable, and in certain cases carbohydrates are entirely replaced by fats. Starch is stored in potatoes and in the tubers of dahlia, and cane-sugar is stored in beet root; the seeds of the two former plants contain oil, while those of the beet are starchy. Although the grains of most grasses contain starch, some instances are known in which fatty oil is present instead (*Phragmites communis*, *Koeleria cristata*, etc.). In the cotyledons of *Impatiens Balsamina* amyloid is stored in the form of enormously thickened walls, while in other species of *Impatiens* the tissue of the cotyledon is thin-walled and oil is present instead of reserve cellulose.

The change of carbohydrates to fats in the seeds of plants has been studied by SCHMIDT (11), LECLERC DU SABLON (4), and others. These investigators have shown clearly that as the

carbohydrates decrease in seeds the fat increases. For instance, when almond seeds first begin to ripen, they are rich in carbohydrates and poor in fats; when fully matured, however, they are poor in carbohydrates and rich in fat. The seeds of *Ricinus* and *Paeonia* are also typical cases. It seems as though the oil in the mature *Ricinus* seed comes from glucose, while that of the *Paeonia* is formed from starch. As it is possible for the plant to translocate fat as such, provided it be an emulsion sufficiently fine, or in the form of fatty acids and glycerine, it might appear to some that the fats in seeds have not been formed *in situ*, but have been conveyed there by the sap. It cannot be denied that translocation of fat may occur to a certain extent; but it is a fact that fats will appear as the carbohydrates disappear in immature seeds even when removed from the parent plant. This fact, when considered with the facts known regarding the formation of fats in vegetative organs under the influence of cold, leads to the inevitable conclusion that fats are formed at the expense of carbohydrates and that this trans-formation may occur *in situ*.

SCHMIDT (11) and LECLERC DU SABLON (4) have shown conclusively that during the germination of oily seeds a reversal of this process takes place, carbohydrates being formed apparently from fat.

The processes by which carbohydrates are changed to fat are still unknown. As the carbohydrates do not contain such complicated carbon chains as the fats, the formation of fat from carbohydrates must consist of a synthesis, in which the CHOH group is converted into CH_2; hence a reduction must occur.

The formation of fat from carbohydrates in the plant has its parallel in the animal. The great influence of carbohydrates on fat formation in the animal was observed and proved by LAWES and GILBERT (5), VOIT (14), LUMMERT (7), and many others by means of a series of nutrition experiments with different animals, with foods especially rich in carbohydrates, who have apparently proved that a direct formation of fat from carbohydrates does actually occur.

The fat of the poison oak fruit is not a reserve food supply for use of the cotyledon; this is shown by morphology and sprouting.

When the drupe is planted, the growing embryo does not utilize the fat, as it remains unchanged. The fat, however, may be of service to the seed as a protection against cold on account of its low power for heat conduction, increasing its chance of dispersal by streams, as it is far lighter than starch (specific gravity of starch 1.56, fat 0.9872); as a protection from rain and humidity; as a protection from fungi (PFEFFER 9); and as an attraction to birds and therefore a factor in seed dissemination. The ripe fruits persist on the plant during the winter, long after the leaves have fallen, some until May. Birds, therefore, can see them for a long distance. When eaten,, the fatty covering of the drupe only is digested; the ejected seeds can still germinate. MÖBIUS (8) has observed the fruits of *R. vernicifera* eaten by half-wild pigeons at Frankfurt. REINECKE (10) has recorded the doves of Samoa as eating the fruit of *R. tahitensis*. BARROWS (1) speaks of the consumption of the fruit of *R. venenata* and *R. Toxicodendron* by the crow. After eating the fruits the crow rapidly digests the nutritious pulp and ejects from the mouth (in less than 40 minutes after eating) the seeds clean and devoid of pulp, together with the sand swallowed to aid in digestion. Of these ejected seeds 90 per cent germinated.

BRYANT (3) has observed that the favorite food of the roadrunner (*Geococcyx californianus*) during the winter season consists of the fruit and seeds of *R. integrifolia*. Unlike many birds which turn their attention to vegetable food during the winter season, the roadrunner appears to discriminate as to the kind of seeds taken. Of the stomachs examined, those of 26 (31.3 per cent) contained the seeds or fruit of *R. integrifolia*, and 8.4 per cent of the food taken by all the birds was made up of this element. The attention of the roadrunner is apparently attracted to this vegetable food only during the winter season, when insects, lizards, and other kinds of food are least abundant.

Summary

1. Substances more similar to Japan wax than to any other fat have been isolated from the ripe fruit of *R. laurina* and *R. diversiloba*.

2. A decrease in the poisonous properties of the fruit of *R. diversiloba* occurs simultaneously with the increase in fat content.

3. The decrease in the poisonous properties in the ripening of the fruit of *R. diversiloba* eventually results in the fruit becoming non-toxic. This phenomenon is not necessarily due to a chemical transformation of the poison into fat for: (a) subsequent to the formation of fat the cells in which it is deposited become filled with starch; (b) it is possible for the plant to transform starch into fat; (c) fat is not formed in the parenchymatous sheaths of the resin passages; (d) consequent upon the formation of fat, the resin passages are everywhere constricted by the growth of parenchyma sheaths; (e) a similar fat has been found in the fruit of a non-poisonous species of *Rhus*.

I am indebted to Professor T. BRAILSFORD ROBERTSON for having placed the resources of his laboratory at my disposal during this investigation.

PASADENA, CAL.

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CURRENT LITERATURE

NOTES FOR STUDENTS

Crown gall.—Recent developments in the study of crown gall and its relation to animal cancer have been presented by SMITH in several papers. The first[1] of these, in point of completion although not in time of publication, is a succinct account of remarkable growth phenomena resulting from the action of *Bacterium tumefaciens* when inoculated into special tissues of plants. Four cases are distinguished.

1. When the internodal cambium is inoculated, this tissue loses its tendency to form mature structures having definite orientation. Instead, the cells continue to divide rapidly, forming large masses of mostly embryonic parenchyma within which scattered and irregularly arranged xylem and phloem elements are differentiated. The process recalls that described by LAMARLIÈRE[2] in the galls of *Gymnosporangium* and aptly designated by him as "parenchymatization."

2. When the cortical parenchyma is infected, a somewhat similar development takes place. The cell divisions succeed each other so rapidly that the cells in the proliferating tissue remain small in comparison with the normal parenchyma, and appear to remain continually in an embryonic state. In time, however, there is a tendency to develop vascular elements, and these are then arranged in a more or less well defined stele. The vascular system of such tumors has no connection with that of the stem, consequently the galls soon die from imperfect nutrition and lack of water. The galls of these two types exhibit no external differentiation. They include all the forms of crown gall described in former papers.[3]

3. A more remarkable condition is brought about when the crown gall organism is inoculated into the leaf axils of young growing plants (species of *Pelargonium*, *Nicotiana*, *Lycopersicum*, *Citrus*, and *Ricinus*). The tumors

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[1] SMITH, ERWIN F., Crown gall studies showing changes in plant structures due to a changed stimulus. Jour. Agric. Research **6**:179–182. *pls. 18–23.* 1916; see also Le cancer est-il une maladie du regne végétal? Premier Congress Internat. Path. Comp. Vol. II. 1912; Cancer in plants. Proc. 17th Internat. Congress of Medicine. Vol. III. Pathology. London. 1913; Further evidence as to the relation between crown gall and cancer. Proc. Nat. Acad. Sci. **2**:443–448. 1916; Further evidence that crown gall of plants is cancer. Science **43**:871–889. 1916; Chemically induced crown galls. Proc. Nat. Acad. Sci. **3**:312–314. 1917.

[2] Rev. BOT. GAZ. **42**:153. 1906.

[3] Rev. BOT. GAZ. **52**:75. 1911; **55**:257. 1913.

thus produced are covered with abortive leafy shoots or with flower shoots if a flower incept has been disturbed. On tobacco plants these teratoid tumors may give rise to secondary tumors similar in nature. These daughter tumors are connected with the parent growths by tumor strands which are quite different in structure and location from those occurring in galls of the first two classes. The tumor strands heretofore described were found in the Paris daisy. They arise in the region of the primary xylem and consist of parenchyma tissue. The new tumor strand found in the tobacco occurs in the cortex. It consists of a concentric bundle with the xylem surrounded by the phloem. The daughter tumors arise at intervals along the strand and often have all the characteristics of the parent tumor.

4. The last case, even more remarkable, results when the young leaves of tobacco plants are infected with the crown gall organism. From such infections on the midrib and lateral veins tumors arise which produce leafy shoots. These tumors the author regards as akin to teratoid tumors in animals. The fact of their development is another proof that any plant cell not fully matured may retain the capacity for developing the whole organism.

In another paper,[4] written for medical readers, the subject of crown gall is discussed in its relation to the problems of human cancer. The general resemblances in mode of growth, cell multiplication, occurrence of tumor strands, and production of secondary tumors in the two classes of growths are pointed out. The materials presented in this paper are essentially those of earlier papers, together with the new facts of the paper reviewed above. The phenomena, however, are described in greater detail, and considered with special reference to their bearing on animal pathology. Here, as in other cases, the author relies mostly on numerous excellent photographs for the presentation of his evidence.

In explaining his standpoint with reference to the bearing of his work on the problems of animal cancer, the author makes no claim that the causal organism of the crown gall has any relation to human cancer. It is pointed out, however, that this organism induces in plants a set of phenomena which have a striking parallel in the manifestations of animal cancer. Such phenomena are the growth without function shown by gall tissue, the persistently embryonic character of the proliferating cells, the lack of orderly differentiation of the tumor tissues, the existence of tumor strands giving rise to daughter tumors repeating the structure of the parent gall, and the occurrence of galls resembling embryonic teratoids. It is further pointed out that in the crown gall the cell, although apparently possessing invasive capacity,[5] is not itself the parasite, as

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[4] SMITH, ERWIN F., Studies on the crown gall of plants; its relation to human cancer. Jour. Cancer Research 1:231–258. *pls. 1–25.* 1916.

[5] It appears that the embryonic tissue of the gall to a certain extent pushes in among the cells of the sound tissue, a phenomenon which distinguishes this growth from other plant galls induced by fungous or animal parasites. The mode of progress

JENSEN thought. On the contrary, the behavior of the cell is due to an invading specific microorganism. These facts, together with the observation that in one case at least (Rous' sarcoma of fowls) the abnormal growth can be produced by some sort of material separable from the cells and capable of multiplying when injected into other tissues, are regarded by the author as greatly advancing the contention that animal cancer is due to an intracellular parasite.

Exceedingly interesting results[6] were obtained in a series of experiments designed to determine the more immediate causes of tumor growth in crown gall. In this investigation the author was guided by the hypothesis that the substances produced in the metabolism of *Bacterium tumefaciens* must be the direct cause of the cell proliferations. To the end of determining the effects of such substances various plants were injected first with compounds which chemical studies had shown to be products of the causal organism, and finally with a large number of other substances.

The first experiments were conducted with ammonia, which in various concentrations was injected into the stem cavity of *Ricinus* and into the fruit cavities of young green tomatoes. The result of these injections was an abundant formation of cushion-like intumescences within the cavities in both cases. Later, proliferations of the same type were obtained by the injection of a large number of other substances, including ammonium salts of organic and of inorganic acids, dilute solutions of the acids themselves, salts, glucose, and saccharose, and in some instances to a slight extent with distilled water. In many cases when the tissues of the pith cavities of *Ricinus* were exposed to weak ammonia vapors from dilute solutions of ammonium phosphate or ammonium carbonate in tubes sealed into the hollow stems, proliferations were produced not only in the cavities containing the reagents but also in many internodes above and below the opened one. The action in these cases, therefore, took place at a distance through thick partitions. The most striking result was obtained from the injection of a 5 per cent solution of ammonium dihydrogen phosphate into a very young internode of *Ricinus*. In this instance the pith cavity became completely filled by the proliferating pith, and from this tissue a complete vascular cylinder was differentiated. The orientation of the new inner cylinder was the inverse of that of the normal cylinder, the phloem being at the center and the xylem occupying the outer region. Such a complete cylinder was observed only once, but in many instances isolated

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of the tumor strand through the tissues is not yet clear. Whether this structure pushes its way through the pith or cortex by apical growth after the manner of the internal roots of lycopods, or whether progress through the tissues is accomplished by successive cell-invasion by the bacteria and subsequent differentiation of the invaded cells into the characteristic tumor strand, has not yet been determined. From study of his stained sections SMITH thinks that both types of invasion occur.

[6] SMITH, ERWIN F., Mechanism of tumor growth in crown gall. Jour. Agric. Research **8**: 165–186. *pls. 4–65.* 1917.

concentric bundles were produced in the proliferating pith. In these the phloem was always at the center of the bundle. Such bundles, the author points out, occur normally in the axes of the inflorescence of *Ricinus* and in the nodes. Superficial intumescences similar to those reported by VON SCHRENK[7] were produced on cauliflower by exposure of the plants to vapors of ammonia and of acetic acid mixed with alcohol.

The outgrowths here described all partake of the nature of intumescences frequently observed in plants. In some cases, indeed, as in the instance described of the complete filling of the pith cavity and the subsequent differentiation of a vascular ring, the outgrowth is excessive. This behavior leads the author to the belief that if the stimulus could be continually applied, one would have a condition resulting in the production of tissue masses not unlike those of crown galls. Since in his experiments the outgrowths also resulted from the presence of many substances not the product of parasites, the author is inclined not to attribute the effect to the specific chemical action of any compound, but seeks for an explanation in some property common to all the compounds regardless of chemical composition. Such a common characteristic he finds in their osmotic action, to which, rather than to chemical stimulation, he ascribes their effect. In this connection it is of interest to recall that intumescences have been produced by ATKINSON,[8] Miss DOUGLAS,[9] and STEINER[10] by subjecting plants to conditions increasing water absorption and diminishing transpiration; and by SORAUER, KÜSTER, VON SCHRENK, and others as a result of application of solutions. In the author's own work the intumescences were mostly the result of injection of solutions, but in some instances they resulted from the injection of water. It is improbable that the osmotic disturbances induced by the application or injection of water are the same as those effected by the application or injection of solutions. The fact that the various disturbances produce responses differing only in degree would seem to indicate that the causes determining the formation of intumescences have not yet been fully analyzed into their separate factors. It is not unlikely that different plants react differently in this respect. The experiments of STEINER would seem to indicate that such a possibility exists.—H. HASSELBRING.

Taxonomic notes.—GATES[11] has attacked the genus *Polygonatum*, which he says "has been in a very chaotic condition owing to the lumping of species, the transference of names, and the confusion of North American with European

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[7] Rev. Bot. Gaz. **40**:390. 1905.

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[9] DOUGLAS, Miss G. E., The formation of intumescences on the potato. Bot. Gaz. **43**:233–250. 1907.

[10] Rev. Bot. Gaz. **40**:391. 1905.

[11] GATES, R. R., A revision of the genus *Polygonatum* in North America. Bull. Torr. Bot. Club **44**:117–126. *pls. 4–6*. 1917.

species." He recognizes 9 North American species, giving under each the full synonymy and citations of exsiccatae. The amount of change is indicated by the fact that the revision includes a new species combination, a new variety, and 3 new variety combinations.

KOIDZUMI[12] has published some studies of the plants of oriental Asia, describing new species and varieties. Notable among the genera is *Morus*, of which 25 species are enumerated, 4 of which are new.

MOORE,[13] in connection with descriptions of numerous new species of African Compositae, has established a new genus (*Paurolepis*) belonging to the Vernonieae.

NAKAI,[14] in continuing his studies of the flora of Japan and Korea, has described 21 new species, mostly in genera familiar in this country. The completed studies will furnish much additional evidence of the close relationship of the Japanese and North American floras.

PAYSON,[15] in studying the American perennial scapose species of *Draba*, recognizes 26 species, 14 of which are described as new. The new species are from Utah, Nevada, California, Oregon, Idaho, and adjacent Canada.

POVAH,[16] in concluding his studies of *Mucor*, has presented a taxonomic description of the 18 species investigated. In view of the fact that his experimental work showed that the species of *Mucor* are usually plastic organisms, varying especially with the substratum, it seemed desirable to attempt a standardization of cultural requirements, by investigating as many species as possible under the same cultural conditions. The 18 species described were studied from uniform, standard bread cultures, and 6 of them are described as new.

SMITH[17] has described a new genus (*Parasyringa*) of Oleaceae from China.

TRANSEAU[18] has published a list of the algae of Michigan, based chiefly upon collections made by him during the summer of 1915, in connection with the Michigan Biological Survey, supplemented by other collections. Since no work on Michigan algae has been published for a number of years, the records

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[12] KOIDZUMI, GENITI, Contributiones ad floram Asiae Orientalis. Bot. Mag. Tokyo **31**:31–41. 1917.

[13] MOORE, SPENCER LEM., Alabastra diversa. XXVII. Jour. Botany **55**:100–106. *pl. 547*. 1917.

[14] NAKAI, TAKENOSHIN, Notulae ad plantas Japoniae et Koreae. XIV. Bot. Mag. Tokyo **31**:97–112. 1917.

[15] PAYSON, E. B., The perennial scapose Drabas of North America. Amer. Jour. Bot. **4**:253–267. 1917.

[16] POVAH, ALFRED H. W., A critical study of certain species of *Mucor*. V. Taxonomic. Bull. Torr. Bot. Club **44**:287–312. *pls. 17–20*. 1917.

[17] SMITH, W. W., Note on *Parasyringa*, a new genus of Oleaceae. Trans. and Proc. Bot. Soc. Edinburgh **27**:93–96. 1916.

[18] TRANSEAU, E. N., The algae of Michigan. Ohio Jour. Sci. **17**:217–232. 1917.

for species are for the most part new to the state. The list includes 226 species, and among them there is a new species of *Oedogonium* (*O. americanum*), and new varieties of *Vaucheria geminata* and *Oedogonium undulatum*.

VAN ALDERWERELT,[19] in continuing his studies of Malayan pteridophytes, has described 27 new species of ferns, among them a new genus (*Campylogramma*), 11 new species of *Lycopodium*, and 7 new species of *Selaginella*.—J. M. C.

Direct reading potentiometers.—The electromotive force of the hydrogen electrode bears a logarithmic relation to the normal hydrogen-ion concentration H+ of the solution. Where large numbers of determinations are concerned, the calculation of the reaction of the solution in terms of normal acidity becomes laborious. An attempt to simplify the process was made by SÖRENSON, who introduced the P_h values. Since the P_h value is the negative logarithm of the hydrogen-ion concentration, the relation existing between these numbers and the usual method of expressing acidity in terms of normality is not always clear.

BOVIE[20] has devised a potentiometer which reads directly in terms of hydrogen-ion concentration. In the original article a full discussion is given of the method of operating the instrument, as well as of the construction of the dip electrode to be used in titrations. This instrument enables the operator to titrate a solution to a definite hydrogen-ion concentration and thus avoid the error due to misjudgment of the end point as found by the indicator method. Another advantage of the instrument is that it makes it possible to titrate two different acids in the same solution or to titrate successively the hydrogen ions of polyvalent acids or acid salts. It also makes possible the titration of such acids as boric acid, which give an end point on the alkaline side of the neutral point of distilled water. The author gives a number of other very useful applications for the instrument. The apparatus is very well adapted for making large numbers of determinations rapidly and with an accuracy sufficient for ordinary purposes.

Using logarithmic resistances instead of the logarithmic scale, BARTELL[21] has devised a similar apparatus, which avoids the sources of error in the BOVIE apparatus and gives a greater accuracy. It is not expected that this type of potentiometer will replace the older forms which are adapted to reading very small potentials.—R. B. HARVEY.

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[19] VAN ALDERWERELT, Capt. C. R. W. K., New or interesting Malayan ferns. 8 and 9. Bull. Jard. Bot. Buitenzorg nos. 23 and 24. pp. 27 and 8. *pls.* 4. 1916 and 1917.

[20] BOVIE, W. T., A direct reading potentiometer for measuring and recording both the actual and total reaction of solutions. Jour. Med. Research **33**:297. 1915.

[21] BARTELL, F. E., A direct reading ionometer. Jour. Amer. Chem. Soc. **39**:630. 1917.

Mottling in citrus leaves.—JENSEN[22] has attempted to see whether there is any relation between mottling of *Citrus* leaves and the supply of nutrient salts necessary for chlorophyll formation. Such was thought possible since the Office of Biophysical Investigations had found that mottling is inversely proportional to the humus content of the soil, and that decomposing organic matter increases the soluble salts in the soil of the groves. The following statements from his summary indicate the results of the investigation: "Judged by a comparison of the average percentages of the inorganic elements determined in healthy *Citrus* leaves and in leaves in the medium stages of mottling, the data obtained did not show that the initial mottling could be accounted for by deficiency in the transfer of the iron, calcium, magnesium, and phosphoric acid from the conducting system of the leaf stem and midrib to the mesophyll tissue. On the other hand, sharply localized yellow areas in old orange leaves contained less of these elements than the adjoining green areas (mostly veins), but whether that relation obtained in the initial stage of mottling was not determined. In very badly mottled *Citrus* leaves there was in general an increase in the percentage of these elements in the conducting tissues, including the leaf stems, indicating difficulty in their transfer to the mesophyll tissues in very advanced stages of mottling, probably because the leaf had become functionless."

The process of mottling is seemingly very complex, involving as it likely does an unusually rapid decomposition of chlorophyll and not merely a cessation in chlorophyll formation. This problem may yield to solution, if at all, only after a many-sided attack. In some of the algae, however, loss of chlorophyll seems to be a direct result of shortage of nitrate supply. Work of this Office seems to exclude this as a possibility in *Citrus* plants, as well as to indicate the complex nature of the process.—WM. CROCKER.

Monocotyledony.—WORSDELL[23] has criticized the reviewer's view of monocotyledony in a paper which "is an astonishing one." In fact, we seem to be mutually astonished, neither being able to understand the reasoning of the other. The paper opens with an account of "an uncommon abnormality," which consists of a "forked coleoptile" in a corn seedling, and this phenomenon is the excuse for the rest of the paper. It may be well to record that this "forked coleoptile" is a very common phenomenon, as all know who have had much to do with corn seedlings in field cultivation.

The author has not realized the facts and significance of zonation, which are fundamental in this connection, and zonation is by no means a "superficial phenomenon." Zonation enables one to realize, for example, that a prominent,

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[22] JENSEN, C. A., Composition of *Citrus* leaves at various stages of mottling. Jour. Agric. Research **9**:157–166. 1917.

[23] WORSDELL, W. C., The morphology of the monocotyledonous embryo and of that of the grass in particular. Ann. Botany **30**:509–524. *figs. 10.* 1916.

projecting stem tip and a meristematic region that later develops such a tip are of the same ontogenetic significance, and therefore that a cotyledonary ring may be lateral even if the stem tip is not organized. The cells that are to organize it later are still apical. It certainly also gives a simpler and more consistent interpretation of the grass embryo than to imagine a cotyledon consisting of such distinct structures as scutellum, epiblast, and coleoptile, distinct in origin as well as in position and appearance. The author disposes of the dicotyledonous embryo of *Agapanthus* as meaning a "progressive" character, from which we are to infer that he still maintains the view that the dicotyledons have been derived from the monocotyledons. We had assumed that this view was no longer under discussion.—J. M. C.

Temperature and viability.—WAGGONER[24] finds that the resistance of radish seeds to high temperature is inversely proportional to the initial water content at the time of heating. At effective temperatures the water content fell with duration of heating. Three different varieties studied showed similar resistance. WAGGONER finds that much of the past work on resistance of seeds to high temperatures lacks precision because the operators allowed the water content to vary greatly during heating. They heated in water in open dishes, in the oven, or in dry corked flasks. The water absorbed or given off by radish seeds during heating as determined by the use of one or the other of these methods goes far to determine their resistance to heat. GROVES[25] has taken care of this source of error by securing his seeds gas-tight in tubes just large enough to hold the 100 seeds, thus leading to a rapid rise of vapor pressure with heating and an equilibrium between the vapor of the air and the water content without measurable water loss. It is interesting to see that radish seeds can be dried down to 0.4 per cent moisture without injury, for EWART[26] has concluded that the sorts of seeds that are most resistant to drying cannot withstand a moisture reduction below 2 or 3 per cent without injury; while *Oxalis*, *Salix*, and *Populus* will not withstand any drying in a desiccator.—WM. CROCKER.

Organic nutrition of plants.—KNUDSON[27] has investigated the influence of certain mono- and disaccharides, added to nutrient media, on the growth of various green plants, as corn, peas, radish, vetch, etc. These plants can absorb through the root system and utilize sugars in growth. The order of the sugars with reference to beneficial effects varied with the kind of plant. Thus with corn grown in the light, the order was glucose and fructose, saccharose, maltose;

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[24] WAGGONER, H. D., The viability of radish seeds (*Raphanus sativus* L.) as effected by high temperatures and water. Amer. Jour. Bot. **4**:299–313. *fig. 1.* 1917.

[25] BOT. GAZ. **58**:169–189. 1917.

[26] Ewart, Proceedings and Trans. of the Liverpool Biol. Soc. **10**:185–193. 1896.

[27] KNUDSON, LEWIS, Influence of certain carbohydrates on green plants. Cornell Agric. Exp. Sta. Mem. **9**:1–75. 1916.

while with Canada field peas it was saccharose, glucose, maltose. lactose. Timothy was found to utilize lactose when grown in darkness, but not when grown in light. The influence of the sugars upon the rate of respiration in the vetch was observed, with the result that saccharose, glucose, and maltose accelerate respiration very noticeably, the latter somewhat less than the other two. Galactose was found to be toxic to wheat, peas, corn, and vetch, even at low concentrations; while glucose antagonizes the toxicity of galactose, possibly by rendering the roots impermeable to galactose, or by altering galactose metabolism in such a way as to prevent formation of toxic oxidation products. The author suggests as a general conclusion that soluble organic substances produced from humus during decay may play a more important rôle in the organic nutrition of plants than we have hitherto thought.—CHARLES A. SHULL.

Osmotic pressure in parasite and host.—Using the cryoscopic method, HARRIS and LAWRENCE[28] have studied the osmotic relations between 7 species of Jamaican mistletoes and their 19 hosts. They find that the sap concentration of the chlorophyllous tissues of the parasite is nearly always higher than that of the mature leaves of the host, the parasites showing an average concentration equivalent to 14.43 and the hosts to 13.59 atmospheres of osmotic pressure. This relationship is not a necessary one, however, for in several cases the parasites possessed sap of a lower concentration than their hosts. In such cases it is assumed that the host supplies more than sufficient water to meet its own needs, so that the parasite is not in direct competition with the leaves of the host, but merely secures water from the same transpiration stream. In cases of secondary parasitism, the osmotic pressure increases from host to primary and from primary to secondary parasite. The sap from the stems of leafless species of *Dendrophthora* possesses a lower concentration than that from leaves of species of *Phoradendron* and *Phthirusa*. The meaning of this is not discussed. It may involve differences in the rate of photosynthetic activity in the leafless and leafy forms.—CHARLES A. SHULL.

Galls.—ESSIG[29] calls attention to the introduction of the chrysanthemum gall fly from Europe. This pest was not known in the United States previous to 1915. It causes cone-shaped galls which often distort the shoot beyond recognition, and eventually causes death of the infected parts. It sometimes destroys one-third of the crop.

WELLS[30] gives us a very important study o the galls of the blackberry The purpose of the paper is threefold: (1) a study of the histology of the galls;

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[28] HARRIS, J. ARTHUR, and LAWRENCE, JOHN V., On the osmotic pressure of the tissue fluids of Jamaican Loranthaceae parasitic on various hosts. Amer. Jour. Bot. **3**:438–455. 1916.

[29] ESSIG, E. O., The chrysanthemum gall fly, *Diarthronomyia hypogaea* F. Low. Jour. Econ. Ent. **9**:461–468. 1916.

[30] WELLS, BERTRAM W., The comparative morphology of the zoocecidia of *Celtis occidentalis*. Ohio Jour. Science **16**:249–290. *pls. 8*. 1916.

(2) a study of the galls of *Celtis occidentalis;* (3) a comparative study of structures. The work is exceptionally well done and well presented. There are 17 known species of zoocecidia on the *C. occidentalis.* The acarinous and lepidopterous galls are kataplasma in character, and the hemipterous and dipterous galls protoplasma in character. This latter type is more closely comparable to the normal plant parts, but the tissue forms are new. The author very properly suggests that zoocecidology presents a unique field for the study of problems pertaining to the mechanism used in the expression of hereditary characters.—MEL. T. COOK.

Germination of rice.—NAGAI[31] has made rather an extensive general study of the germination of rice, touching many points that have previously been worked out on other seeds. The cutinized inner integument of the ripe fruit is a semipermeable membrane. Such membranes have been found in the fruit walls of many grasses and in the coats of many seeds.[32] Desiccated seeds of rice are not injured by steeping for 24 hours in ether, chloroform, absolute alcohol, acetone, and other substances. This is in accord with the work of BEQUEREL and of SHULL,[33] who have found that the dry coats of many seeds are impervious to such substances, but that, as the water content of the coats rises, they become more pervious. Rice germinates in an extremely low partial pressure of oxygen, yet the germination is abnormal, the hypocotyl growing only under considerable oxygen pressure. Acids and bases show no stimulative effects upon the germination of rice. A few hours of exposure to liquid air does not injure the seeds of rice or buckwheat. Two hours' exposure to 97–98° C. kills *Zea Mays*, but does little injury to rice, especially if it is desiccated.—WM. CROCKER.

Alkalies and salt absorption.—As a phase in the analysis of the effects of alkalies upon the development of plants, BREAZEALE[34] has studied the effect of NaCl, Na_2SO, and Na_2CO_3 upon the absorption of nitrates, phosphates, and potash by wheat seedlings. Up to 1000 ppm. in a nutrient solution they do not affect the absorption of nitrates. In this concentration NaCl does not modify phosphate absorption, but slightly depresses potash absorption. In 1000 ppm., Na_2SO_4 depresses the absorption of potash and phosphoric acid to approximately 70 per cent of that of the checks. In equal mol concentration Na_2CO_3 depresses the absorption of potash to 20 per cent and phosphoric acid to 30 per cent normal. With Na_2SO_3 these depressing effects were evident in 300 ppm. The writer thinks the depressing effect of the Na_2SO_4 is due to its

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[31] NAGAI, ISABURO, Some studies on the germination of seeds of *Oryza sativa*. Jour. Coll. Agric., Imperial University Tokyo **3**:109–155. 1916.

[32] BOT. GAZ. **56**:169–199. 1913; **63**:373–397. 1917.

[33] BOT. GAZ. **56**:169–199. 1913.

[34] BREAZEALE, J. F., Effect of sodium salts in water cultures on the absorption of plant food by wheat seedlings. Jour. Agric. Research **7**:407–416. 1916.

reaction with $CaCO_3$ of the substratum, thus forming Na_2CO_3. Extensive studies of this sort can add much to our knowledge of the absorption of salts by plants and the intereffects of salts upon each other as regards absorption.—Wm. Crocker.

Calcium compounds of the soil.—Under this title[35] E. C. Shorey, W. H. Fry, and W. Hazen, members of the Bureau of Soils, have analyzed 63 soil samples of 23 types from 24 locations of 19 states. They have calculated the percentage of calcium combined with humus compound, calcium carbonate, calcium sulphate, and calcium as difficultly and easily decomposed silicates. They find a wide variation in total calcium content and in calcium carbonate and the two classes of silicates, and there was no constant relation between the total calcium content and the percentage of any of the calcium compounds. Calcium combined with humus compounds was absent in 29 soils. One type which is recognized as a good alfalfa soil is characterized by high calcium content, but low content of calcium carbonate. This indicates, as does other evidence, that alfalfa requires a rather high content of calcium ion as a nutrient or balancer of the soil solution, rather than merely calcium carbonate as a neutralizer of acidity.—Wm. Crocker.

Phylogeny of ferns.—Bower,[36] in continuation of his phylogenetic studies of the ferns, has developed some interesting conclusions in reference to what he calls the "acrostichoid condition," meaning the spreading of exposed sporangia "uniformly over a considerable area of the sporophyll." This fact was the basis of the old genus *Acrostichum*, which Bower has come to regard not as a natural genus, but as a state or condition which may have been attained along a number of phyletic lines. In the present paper he has presented a number of genera which he regards as "dipterid derivatives," that is, derived from a phyletic stock characterized by *Dipteris*, which show various stages of advance toward the acrostichoid condition. According to this view, a number of so-called genera of ferns are form genera, not being what Bower calls "phyletic unities." The increasing evidence of parallelism in evolution is raising the question of "phyletic unity" in connection with all of our larger genera.—J. M. C.

Pine forests of Virginia and the Carolinas.—Harper[37] recently devised a method for securing a rough quantitative analysis of vegetation from notes taken at frequent intervals from the car window or while walking through the country. He made such notes during 53 hours of railroad travel and 21 hours

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[35] Jour. Agric. Research **8**:57–77. *1917.*

[36] Bower, F. O., Studies in the phylogeny of the Filicales. VI. Ferns showing the "acrostichoid" condition, with special reference to dipterid derivatives. Ann. Botany **31**:1–39. *pls. 1, 2. figs. 15.* 1917.

[37] Harper, R. M., Geography and vegetation of northern Florida. Ann. Rep. Fla. Geol. Survey **6**:163–437. 1914.

of walking in Virginia and the Carolinas. To obtain the relative abundance of species in the area involved[38] he counted the number of times each species was mentioned in the notes, and multiplied the figures for *Pinus Taeda* and *P. palustris* by 5, and for the other conifers by 3 before calculating the percentages. The figures for smaller trees were divided by 2 or by 10, for shrubs by 100, and for herbs by 500. The results were tabulated and are rather interesting. Some estimates of annual increment of the whole vegetation, of the amount of mineral matter taken each year from the soil, and of the amount of water transpired are based upon these analyses.—GEO. D. FULLER.

Forest sanitation.—In a recent bulletin MEINECKE[39] emphasizes the importance and also the difficulties of giving phytopathology a proper place in forest regulation. He elaborates methods of investigation and application, exemplifying by an actual study of *Abies concolor*. Forest sanitation is the keynote of the remedial measures proposed, a system of forest regulation which will give proper attention to the removal or destruction of diseased individuals from the community.

It is also interesting to note that WEIR,[40] after discussing the character and nature of the injuries due to various mistletoes, outlines methods of forest sanitation consisting of directing cutting so as to effect the removal of diseased communities and individuals. Such methods of forest sanitation he believes will become increasingly practicable with the increasing demand for cutting privileges in the National Forest Reserves.—GEO. D. FULLER.

Michigan sand dunes.—In a recent bulletin SANFORD[41] estimates that sand dunes stretch for over 400 miles along shore lines of the state of Michigan and cover not less than 550 square miles of its territory. In the southern peninsula, with the removal of the forests, many of the dunes are becoming active again and now constitute a menace to valuable fruit growing lands. The importance of maintaining a forest cover is pointed out, and the various recognized methods of dune reclamation are described. The failure of certain efforts to control dune movement by planting is shown to be due to a discontinuance of work before the final cover of permanent forest growth becomes established. Such plantings made by the government at Manistee in 1902 resulted in a temporary cover, which a small amount of subsequent planting

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[38] HARPER, R. M., A quantitative, volumetric, and dynamic study of the vegetation of the *Pinus Taeda* belt of Virginia and the Carolinas. Bull. Torr. Bot. Club **44**:39–57. 1917.

[39] MEINECKE, E. P., Forest pathology in forest regulation. U.S. Dept. Agric. Bull. 275. pp. 63. 1916.

[40] WEIR, J. R., Some suggestions on the control of mistletoe in the national forests of the northwest. Forest Quart. **14**:567–577. 1916.

[41] SANFORD, F. H., Michigan shifting sands: their control and better utilization. Mich. Agric. Coll. Exp. Sta. Bull. 79. pp. 31. *figs.* 22. 1916.

would have converted into a permanent forest. A neglect of this attention resulted in the complete failure of the project.—GEO. D. FULLER.

Nitrogen relations of semi-arid soils.—MCBETH[42] finds that semi-arid soils fail to nitrify dried blood when it is added in 1 per cent quantities. Under the conditions ammonia accumulates in the soil and 50 per cent of the nitrogen may be lost to the air (probably as ammonia) within 6 weeks. When added at ordinary fertilizer rates nitrification is complete. With green manures, especially legumes, nitrification is rapid. Fifty per cent of the nitrogen of the green manure is transformed to nitrates in 30 days. Furrow irrigation leads to the accumulation of the larger part of the nitrate in the surface 6 inches of the soil, and this often results in niter spots. Overhead or basin irrigation gives far better results. Mottled orange leaves show higher water content than checks, and extreme mottling is often, yet not invariably, associated with high nitrate content.—WM. CROCKER.

Effect of dust on photosynthesis.—The effect of surface films and dusts on physiological processes in plants has aroused considerable interest in recent years. California citrus vegetation in the neighborhood of cement works becomes covered with cement dust. Since the dry season lasts several months, the dust remains on the leaves for long periods. YOUNG[43] took advantage of this fact to determine the effect of dusts on carbohydrate synthesis. He found that the cement dust in some cases shuts out as much as 80 per cent of the light from the upper surface of the leaf, but this high exclusion of light did not interfere with carbohydrate synthesis. This work bears out in a practical and interesting way that of BROWN and ESCOMBE in showing the small amount of light that is really necessary for carbohydrate synthesis.—CHAS. O. APPLEMAN.

Nitrogen fixation.—The question of nitrogen fixation by filamentous fungi has been investigated by DUGGAR and DAVIS[44] with reference to *Aspergillus niger*, *Macrosporium commune*, *Penicillium digitatum*, *P. expansum*, *Glomerella Gossypii*, and *Phoma Betae*. Of these, *Phoma Betae* was the only form which was definitely shown to be capable of fixing free nitrogen. The quantities fixed by this fungus varied from 3.022 to 7.752 mg. per culture of 50 cc. of solution when sugar beet or mangel decoction with added sugar were used as culture media. The authors give a critical review of all the available literature on the subject, and in their own work exercised every precaution to avoid the errors and faulty methods which have led to the numerous conflicting results in the investigations of this problem.—H. HASSELBRING.

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[42] MCBETH, I. G., Relation of the transformation and distribution of soil nitrogen to the nutrition of citrus plants. Jour. Agric. Research **9**:183–252. *figs. 19.* 1917.

[43] YOUNG, H. D., Studies on the relation of cement dust to citrus vegetation. I. The effect on photosynthesis. Biochem. Bull. **5**:95–100. 1916.

[44] DUGGAR, B. M., and DAVIS, A. R., Studies in the physiology of the fungi. I. Nitrogen fixation. Ann. Mo. Bot. Gard. **3**:413–437. 1916.

Himalayan vegetation.—Among the matters of botanical interest STEWART[45] has emphasized is the absence of all luxuriant tropical vegetation from this part of India, the indigenous flora being rather of the desert and scrub types. Perhaps the most interesting thing concerning this little known region is the similarity of the forests on the north side of the mountains to those of the eastern United States, as shown by the abundance of trees of such familiar genera as *Pinus*, *Picea*, *Abies*, *Taxus*, *Juglans*, *Betula*, *Ulmus*, *Prunus*, *Acer*, *Quercus*, *Populus*, and *Berberis*. Set in strong contrast are the most abundant genera upon the corresponding southern slopes. This aggregation includes *Acacia*, *Capparis*, *Tamarix*, *Zizyphus*, *Melia*, *Albizzia*, and *Olea*.—GEO. D. FULLER.

Mycorrhiza of Marattiaceae.—WEST[46] has made a careful study of the life history, host relations, and systematic position of a fungus long known to be present in the roots of the Marattiaceae. It is one of the Phycomycetes, and most nearly approaches *Phytophthora* in such characters as are available, but the sexual organs were not observed. WEST has established a new genus (*Stigeosporium*) to include it. No injury to the cells of infected roots by the parasite could be recognized, and the resting spores, with their oily contents, are also formed at the expense of the host. "The advantage of the association is almost entirely on the side of the fungus, the host plant thriving in spite of the presence of the endophyte."—J. M. C.

Cambium in monocotyledons.—MRS. ARBER[47] has brought together the scattered observations of the occurrence of an ephemeral intrafascicular cambium in monocotyledons, and records also some new observations. It is clear that such a cambium occurs more widely among monocotyledons than has been generally supposed. To the previously recorded cases she adds the inflorescence axes of *Eremurus himalaicus* and *Nothoscordum fragrans*, and the young shoots of *Asparagus officinalis*. The widespread occurrence of this "vestigial, intrafascicular cambium" is a strong additional argument in favor of the derivation of monocotyledons from dicotyledons.—J. M. C.

Seedling anatomy of Ranales.—Miss BLACKBURN[48] has investigated the seedling anatomy of a large number of the Ranales, chief attention being given to the Ranunculaceae. The results of chief phylogenetic interest are the

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[45] STEWART, RALPH R., Some observations on the flora of northwest Himalaya. Torreya **15**:215–260. *figs. 4.* 1915.

[46] WEST CYRIL On *Stigeosporium Marattiacearum* and the mycorrhiza of the Marattiaceae. Ann. Botany **31**:77–99. *pl. 3. figs. 9.* 1917.

[47] ARBER, AGNES, On the occurrence of intrafascicular cambium in monocotyledons. Ann. Botany **31**:41–45. *figs. 3.* 1917.

[48] BLACKBURN, KATHLEEN B., On the vascular anatomy of the young epicotyl in some Ranalean forms. Ann. Botany **31**:151–180. *pl. 13. figs. 19.* 1917.

general prevalence of the trilacunar trace in the seedlings, and the almost universal occurrence of a single ring of bundles connected at a very early age by cambium. This interfascicular cambium is usually absent in the adult stems of the herbaceous Ranunculaceae, but it is invariably present at some stage in the seedling. The evidence of the origin of herbs from woody plants is increasing.—J. M. C.

Germination of ascospores.—BRIERLY[49] has experimented with the germination of the ascospores of *Onygena equina*, a fungus occurring on decomposing horns and hoofs of cattle, sheep, etc. The results showed that "ripe" ascospores will germinate directly after a prolonged resting period, and that this period may be curtailed or eliminated by treating the spores with artificial gastric juice, but not by subjection to low temperatures. "The full-grown unripe ascospores and the chlamydospores will germinate immediately in the absence of digestive treatment."—J. M. C.

Respiration.—APPLEMAN[50] has investigated quantitatively the relation of oxidases and catalase to the process of respiration in potatoes. He found that there was no correlation between intensity of respiration and oxidase activity, but that catalase activity of the extracted juice of the potato shows a close correlation with the respiratory activity of the tuber. He considers, therefore, that the oxidases are not the controlling factor in respiratory intensity, at least in potato tubers, whatever rôle they may have in connection with biological oxidations.—CHARLES A. SHULL.

History of forest ecology.—In a rather extensive review of the literature of botany and of forestry investigations, BOERKER[51] has attempted to trace the influence of both upon the development of the new phase of science known as forest ecology or silvics. Perhaps the most important part of the paper is that in which he traces the ecological principles which were stated by some of the earlier leaders in forestry, but which have received little attention from their fellow foresters. Of almost equal importance is the rather extensive bibliography.—GEO. D. FULLER.

Wandering tapetal nuclei.—PICKETT[52] has described in detail the differentiation of the tapetum and its subsequent behavior in *Arisaema triphyllum*

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[49] BRIERLY, WILLIAM B., Spore germination in *Onygena equina* Willd. Ann. Botany 31:127–132. 1917.

[50] APPLEMAN, CHARLES O., Relation of oxidases and catalase to respiration in plants. Amer. Jour. Botany 3:223–233. 1916.

[51] BOERKER, R. H., A historical study of forest ecology; its development in the fields of botany and forestry. Forestry Quarterly 14:380–432. 1916.

[52] PICKETT, F. L., The wandering tapetal nuclei of *Arisaema*. Amer. Jour. Bot. 3:461–469. *pl. 20. figs. 8.* 1916.

and *A. Dracontium*. The tapetal cells early show peculiarities of cell wall, cytoplasm, and nucleus. The wall entirely disappears, and the freed protoplasts form a "periplasm" that spreads through the cavity of the sporangium. The forms assumed by the tapetal nuclei, as well as their peculiarities of structure, suggested the possibility of "active migration among the developing pollen spores."—J. M. C.

Vermont trees.—One of the most recent additions to the rather large series of tree manuals is from Vermont.[53] It closely resembles that from Michigan previously reviewed,[54] but it has been revised and modified to meet the slightly different conditions in the new region. There are two sets of keys, one for winter and another for summer use. These, together with the illustrations, should make the identification of any tree an easy matter.—GEO. D. FULLER.

Fossil Sequoia from Japan.—Miss YASUI has[55] described a new species of *Sequoia* (*S. hondoensis*) from a coal field of Japan belonging to the Tertiary. The genus was recognized, not only by its normal structural features, but also by characteristic wound reactions. This discovery adds to the evidence of the wide distribution of *Sequoia* during the Tertiary, and also adds testimony to the assertion that *Sequoia* has descended from the *Pityoxylon* type.—J. M. C.

The vegetation of New York State.—BRAY[56] has compiled a useful description of the vegetation of New York State, seen from the viewpoint of an ecologist. The state is divided into zones according to MERRIAM'S system, and a map showing the modifications of the zones resulting from differences in altitude and the changes due to soil and to proximity to the Great Lakes is produced. The various forest types are well described.—GEO. D. FULLER.

Anatomy of epiphytic orchids.—CURTIS[57] has published a detailed account of the anatomy of 6 epiphytic orchids from New Zealand. Considerable variation is shown in the extent and distribution of the different tissues, and the paper is full of data that will be useful when the anatomy of orchids comes to be organized.—J. M. C.

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FOOTHILLS VEGETATION IN THE COLORADO FRONT RANGE

CONTRIBUTION FROM THE HULL BOTANICAL LABORATORY 237

ARTHUR G. VESTAL

(WITH EIGHT FIGURES)

The coniferous forests of the Rocky Mountains are fairly well known; the other plant associations have been little studied. In the present account descriptions are given of typical representations of the plant communities of the foothills zone. The area is confined to the eastern slope of the Rockies in Colorado. By the foothills zone is meant the lower elevations, from the plains at 5000–6000 ft. to the middle slopes at 7500–8000 ft. The vegetation zones of the Colorado mountains have been characterized by RAMALEY (**10**). A large part of the field study has been made in the area just west of Boulder, during three years' residence at the University of Colorado; the other parts of the region have been studied on numerous visits, chiefly to stations at or near the mountain-front, from the Big Thompson River as far south as Raton, New Mexico. This article is the second of a series dealing with the vegetation and plant geography of the eastern mountain-front in Colorado. The first account (**24**) is of the plains and prairie associations of the region. The writer is indebted to Professor FRANCIS RAMALEY for many kindnesses and for help in different ways.

Grassland in the Rocky Mountains has a much more important rôle than is usually accredited to it, particularly in the lower slopes.

It is perhaps the conspicuousness of the trees, especially in distant views and in profiles of slopes (fig. 8), which gives the common but not wholly true impression that the foothills are generally forested with conifers. The rock pine, the most generally distributed conifer of the region, forms relatively few and scattered true forests; it usually grows in very open formation, in mixture with the grassland which covers most of the surface. The general aspect of the vegetation is that of an open growth of grassland and scattered pines over a dry and partly bare upland of granitic hills. Semi-mesophytic and mesophytic communities, of both herbaceous and woody plants, occur; but only locally, in moister or more sheltered ravines and canyon-bottoms. The vegetation complex of the mountain-front is a modification of that of the foothills, but is less simple in composition.

Environmental conditions

The Front Range in Colorado is an up-arched and dissected plateau of crystalline rocks, the tops of most of the hills forming the remains of a peneplaned surface; scattered higher mountains represent monadnocks surmounting the former general level. The eastern part of the plateau slopes gently toward the plains, the sedimentary strata of which are here upturned against the granitic rocks, forming sloping crags on the outer face of the foothills, or hogback ridges separated from the hills by north-south valleys. The physical geography of the Front Range is described by DAVIS (5). It is with the lower, more easterly part of the granitic plateau and with the more irregular country of the mountain-front that this study has to do.

The climate of the foothill region is dry, though not enough so to be called semi-arid, like that of the plains. Rainfall at the mountain-front is from about 15 to 18 inches average for the year; higher in the northern part of the state and on the elevated Platte-Arkansas divide, lower south of the Arkansas River. The upper foothills receive about 18–20 inches. Annual variation of rainfall is considerable. Most of the rain comes during the growing season. At Boulder, and in the northern foothills generally, April and May are the rainiest months; in the southern foothills the earlier part of the summer is drier than later. This, with higher summer

temperatures and probably greater insolation, gives a drier aspect to the southern foothills; pinyons are abundant, instead of rock pine, as in the northern part of the state. Mean annual temperatures in the foothills vary from 40 to 50° F.; mean summer temperatures 60 to 70° (ROBBINS 17). Evaporating power of the air is great, though much less than on the plains. Local variations in atmospheric conditions, due to surface configuration, are considerable. Insolation is much greater on summits and south-facing slopes than on north-facing slopes or in ravines. The drying winds are usually from the west, and their effects are greatest on summits and the flatter uplands.

Local and topographic factors are extremely and very locally variable. Position with reference to surroundings, and slope, its amount and direction, may perhaps be called the two master factors of the topographic complex. Slope and position are most important in determining conditions of soil deposition or removal (consequently depth and texture of the soil); conditions of absorption and run-off, drainage, or seepage from above, or possible seepage from snowdrifts; presence or absence of plant remains, which may contribute humus, or locally form a mulch (pine needles); and conditions of exposure to sun and wind with its attendant effects. The granitic hills in general (fig. 1) are in an early-mature stage of topographic development (for a mountain region of resistant rocks); the side-slope profiles are nearly straight, with comparatively little detritus covering the bottom of slopes; the tops of the hills are usually rounded, and hardly more subject to erosion than the sides. In general, the foothills are so well drained that bogs, marshy flats, and moist-soil meadow areas are infrequent, even in canyon-bottoms. Hilltops and side-slopes are covered, usually thinly, with rock-débris or with decomposed granite soils, varying in texture from coarse gravelly material of angular fragments[1] to fine black loamy humus. Wide dikes and occasional outcrops of more resistant rock have only a little soil, in joints and crevices, hardly any elsewhere.

[1] The writer has not been able to find a distinctive name for this coarse angular débris resulting from decomposition of granite; it is not gravel in the sense the word usually implies; in this article it will be called "granite-gravel."

Texture of soil in its influence on water relations is probably the most important soil factor in the foothills, so far as local distribution of plants is concerned. Especially interesting are some of the features of mixed soils, in which fragments of greatly different sizes are intermingled. Rocks of all sizes may occur on the surface, or buried among finer fragments as rock-débris of detrital slopes. Where the large fragments are imbedded beneath the surface in fine soil, the water content of the latter appears to be increased.

FIG. 1.—General view in foothills, looking westward to snowy range-crest; foreground a north slope; general vegetation grassland with scattered pines; southwest of Boulder, 7200 ft.

Where the large rocks are exposed at the surface, moisture conditions appear to be more favorable immediately beside and under them, so that comparatively mesophytic plants are seen growing in mixture with xerophytes, the former always growing beside or from under the surface rocks. This effect will be noticed in the lists of species; many plants are found in both xerophytic and mesophytic assemblages.

The more frequently recurring combinations of topographic and atmospheric factors which form effectively different local environments for plants may be viewed in the synopsis which follows. It is intended to apply only to the foothills proper; a number of situations of the mountain-front belt cannot be included herein.

CLASSIFICATION OF FOOTHILLS HABITATS

Xerophytic habitats (the general condition of summits and side-slopes)
  Rocky habitats
    Craggy summits and rock-walls (see figs. 2, 3)
    Rock-strewn detritus slopes
    Rock-talus, usually less stable than preceding
  "Granite-gravel" habitats
    Compacted granite-gravel floors and side-slopes (see fig. 3)
    Loose granite-gravel floors, washes, and talus (= gravel slides)
  Fine-soil habitats
    Mixed-soil floors and detritus-slopes (fine soil with imbedded and superficial rock fragments of various sizes)
    Fine-soil floors and detritus-slopes (infrequent)
Less xerophytic habitats (valleys and steep slopes, etc., relatively local)
  Less xerophytic side-slopes (mostly north-facing, usually of considerable gradient, and best developed in valleys)
  Mesophytic ravine habitats
    Narrow ravines (best developed in small side-canyons, especially on the south side of eastward-flowing main streams)
    Canyon-bottoms (the wider bottoms of the larger canyons are sometimes, however, exposed and xerophytic)
  Seepage and dripping areas (infrequent and small)
  Stream-side habitats (with usually constant supply of soil moisture, but widely varying atmospheric conditions)

Synopsis of plant associations

The following synopsis is aimed to give in perspective the distinguishing characters of the plant communities of the foothill region. It is based upon whatever features of the particular community seem most distinctive and appropriate: growth-form, moisture relations, physiographic, geographic, and successional relations.

CLASSIFICATION OF FOOTHILLS ASSOCIATIONS

Associations generally primitive in character: the first vegetation of new or unfavorable habitats, usually in rocky or gravelly situations; vegetation open and sparse, generally xerophytic
  Plants lichens; on rock surfaces, either on craggy summits, knobs, and rock-walls, or on loose boulders ..... *Lichen associations*
  Plants spermatophytes, in rocky or detrital situations, soil of variously coarse texture
    Dominant plants shrubs; of relatively local and temporary occurrence; frequent in areas recently denuded ..... *Sumac association*
    Dominant plants herbaceous ..... *Foothills primitive grassland association*

Associations generally intermediate or established in character (usually subsequent to primitive associations, but often in habitats apparently little modified from the primitive condition); soil often of mixed or fine texture, or with considerable humus content; vegetation usually less open and sparse than in preceding

Typically developed in xerophytic or semi-xerophytic habitats, which are of general occurrence in the foothills region (these associations are consequently extensive)

Dominant plants evergreen trees; usually in rocky or coarse soil

Of relatively less xerophytic character; generally distributed in the foothills region . . . . . *Rock pine association*

Of relatively more xerophytic character; of lower and (east of the range-crest) more southerly distribution than preceding

Pinyon-cedar association

Dominant plants deciduous trees or large thicket-forming shrubs; of southerly distribution east of the range-crest; frequent in fine soil, and ranging into less xerophytic habitats . . . . . *Quercus association*

Dominant plants shrubs

Shrubs tall and loosely branched, occurring mostly at and near the mountain-front, in coarse or rocky soils . . . . . *Cercocarpus association*

Shrubs low, creeping and densely branched, occurring mostly in the foothills proper

Plants evergreen, of northerly distribution, more frequent in the higher foothills . . . . . *Arctostaphylos association*

Plants deciduous, of more southerly distribution, more frequent in the lower foothills . . . . . *Ceanothus association*

Dominant plants herbaceous; vegetation grassland, composed mostly of xerophytes

Dominant plants including plains short-grasses of surface-rooted habit; plant population large and diverse, *Foothills mixed grassland association*

Dominant plants mostly tufted bunch-grasses of deeper-rooted habit

Bunch-grass association

Typically developed in mesophytic or semi-mesophytic habitats (which are much less extensive in the foothills than xerophytic habitats, being represented chiefly on north slopes and in ravines and canyons)

Dominant plants evergreen trees . . . . . *Pseudotsuga association*

Dominant plants deciduous trees

Typically developed along stream margins in open canyons

Populus-Salix stream-side association

Typically developed in less exposed situations than preceding, as bottoms of V-shaped ravines and moist shaded slopes

Canyon forest association

Typically developed in moist ravines or slopes with humus soil; or, in the higher foothills, in moist patches of the granite-gravel upland

Aspen association

Dominant plants shrubs, or rarely reaching tree size
Plants larger, comparatively well separated; plant composition variable; ranging also into xerophytic habitats
Foothills mixed shrub association
Plants smaller, low, closely set, usually in fine moist soil
Symphoricarpos association
Dominant plants herbaceous. . . . *Foothills mesophytic grassland association*

Descriptions of associations

The plant communities are described in the order of their appearance in the foregoing synopsis. They are subject to greater geographic variation than can be treated fully in this article; mention is made, however, of the more considerable variations. The space allotment is not always proportionate to the importance or general interest attaching to the several associations; some are already fairly well known, some are less variable or can be summed up more concisely than others, and some have been less thoroughly or less widely studied. An approach to a balanced treatment has been sought by the use of a smaller type for statements of less general significance, descriptions of minor or very local vegetation divisions, and detailed passages included by way of illustration or amplification.

Plant names, when appearing without citation of authorities, may be understood to be as in COULTER and NELSON'S *Manual* (**2**), which in general follows the usage recommended by the Vienna Congress. The unit of vegetation is the plant association, in the generally accepted sense; its distinctive representations, appearances, or variants are spoken of as consocies; the terms as used are described in an earlier article (**24,** p. 382, footnote). Index letters attached to species names signify frequency or abundance or regularity of occurrence, as follows: *a*, abundant; *f*, frequent; *i*, infrequent; *l*, local or locally; *ch*, characteristic in the community or situation mentioned.

It will be understood that the total number of species of plants occurring in an area so extensive as that of this study is very large. No attempt has been made to work out the complete floristics, or the floristic variation of the several communities as represented in different localities. Field botanists will remember that very many of the species making up the flora of a region are rare, known from a single or very few stations, are in effect of very slight ecological significance, so far as vegetation is concerned. A further considerable proportion is not found in extensive plant assemblages (as, in this study, grass species occurring only in stream margins), and is not important as part

of the vegetation of the general area. Several or numerous species of certain genera, again, may be of similar habitat distribution, so that a species of one locality may be replaced in the same habitat in another locality by a second species of that genus. Care has been taken to select species for the floristic lists which are as representative over a considerable area as may be. In the southern foothills, as in the plains of southern Colorado, many more plants of southwestern derivation enter into the flora, particularly in the primitive grassland and mixed grassland assemblages. Many are true desert plants; a few cacti and chenopods and many composites fall in this group. That this geographic variation from north to south is ecological as well as floristic should be apparent. It is paralleled by a similar altitudinal variation in composition, from the montane zone to the plains.

LICHEN ASSOCIATIONS

TUCKERMAN (**23**); WILLIAMS (**27**), lichens in the Black Hills; HERRE (**7**), lichens of Mount Rose, Nevada; SHANTZ (**22**, p. 187).—Fig. 2.

A considerable proportion of the area of the foothills is exposed rock, and its vegetation, except in crevices, is mostly composed of lichens. The study of lichen vegetation has usually been left to the specialists in that group of plants, since they are so poorly known to most other botanists. For this reason brief notes on external appearance, as to color and vegetative form, are given with the species names. The writer is indebted to R. HEBER HOWE, Jr.,[2] who has made the species determinations and examined this part of the manuscript (fig. 2).

Dry surfaces, much exposed to sun and wind, occupy most of the area of bare rock in the foothills. They slope considerably, so that run-off is rapid and absorption minimal. The first lichens to invade dry rock, forming primitive xerophytic stages of lichen growth, are fine-grained crustose forms, notably the black-gray *Rinodina radiata* Tuck. (?=*R. thysanota* Tuck.) and an indeterminable lead-gray species which is especially characteristic. These are soon followed, but not displaced, by lichens of an intermediate stage, mostly coarser crustose forms; the gray-green *Rinodina oreina* (Ach.) Wain. is a character species both locally and geographically abundant. The established stage on dry rock is marked by the gray-green small-foliose *Lecanora rubina* (Vill.) Wain. and the

[2] Some of the crustose species were determined for Dr. HOWE by H. E. HASSE; the *Stereocaulon* by L. W. RIDDLE.

larger-foliose, also gray-green, *Parmelia conspersa* (Ehrh.) Ach., which may be said to be the dominant and most frequent lichen of exposed rock. Here also occur the gray-green crustose-foliose *Rhizocarpon geographicum* (L.) DC., with *Rinodina oreina* persisting from the preceding stage, and a few other species, including one or two of *Parmelia*, *Gyrophora erosa*, and the large and peculiar *Gyrophora vellea* (L.) Ach., in crisped-margined dirty-gray plates 0.25–2 inches in diameter, attached centrally beneath. These

FIG. 2.—Lichens on steep rock-wall of rather sheltered side-canyon opening northward into Boulder canyon; dark masses at joints are cushions of *Selaginella*.

established stages appear to be self-perpetuating so long as physical conditions of dry rock are unchanged.

Less exposed, but usually dry, surfaces, such as shaded rocks, overhangs, surfaces dripping for some time after rains, recesses in joints, etc., have also characteristic lichen assemblages and definite successions. The earlier lichens include the yellow-green crustose *Acarospora xanthophana* (Nyl.) Fink (characteristic and abundant), with *Lecanora rubina*, *Rhizocarpon geographicum*, and *Rinodina radiata*. *Acarospora* persists in the established stages, which also show the bright orange-brown crustose-foliose *Caloplaca elegans* (Link.) Th. Fr. (characteristic and abundant), *Parmelia conspersa*, *P. sulcata* Tayl., *P. conspersa* var. *stenophylla*? Ach., *Gyrophora vellea*, and other species. Considerably less of the rock surface remains uncovered with lichens here than in the xerophytic situations, and the number of species is larger, although the area of this

habitat and its lichen assemblage is very much smaller. *Caloplaca elegans* and *Parmelia sulcata* are frequent on scattered rocks and tree trunks in shaded canyon-bottoms.

Moist surfaces in humid recesses of the rocks show numerous lichen species, mostly foliose, including *Physcia aipolia* (Ach.) Nyl. and a number of species of *Parmelia*. Mosses grow with the lichens abundantly in these situations. These distinctly humid recesses are scattered and infrequent in the foothill region. A *Cladonia*, probably *C. fimbriata* (L.) Fr., is characteristic on moist north-facing canyon slopes, amongst mesophytic herbs, or beside surface rocks. A pulvinate, finely divided whitish fruticose lichen, *Stereocaulon albicans* Th. Fr., has the growth-form of a pulvinate moss, being "rooted" in moist rock crevices, although the aerial part is more or less exposed. It is infrequent.

SUMAC ASSOCIATION

ROBBINS (**16,** p. 46), distribution on Long Mesa near Boulder.

As indicated in the synopsis of associations, the shrubs of sumac (*Rhus cismontana* Greene, which is so like *R. glabra* of the eastern states as to be considered identical with it by some botanists) often form a new plant assemblage in denuded xerophytic situations. These are extremely variable, including old roadways, rock talus below road embankments, quarries, or prospect holes, stony hillsides where erosion or landslipping has removed much of the plant cover, or places which have been burned. In the lower foothills, and at the mountain-front, the sumac appears to be quite common after fires, the slopes being too dry to allow the establishment of aspens, in most places. The shrubs are usually separated, the sparse plant cover of the interspaces often being composed of plants of the primitive grassland association. As developed in the foothills, the assemblage shows no essential difference from the sumac growths of many parts of the United States. In autumn the bright red coloring of the leaves makes the community very conspicuous, so much so as to give an exaggerated notion of its frequence of distribution.

FOOTHILLS PRIMITIVE GRASSLAND ASSOCIATION

CLEMENTS (**1,** pp. 9–12), gravel slide formation, half gravel slide formation, in part; RAMALEY (**12,** pp. 124–128), *Cercocarpus* scrub, upland dry grass, and foothill sagebrush-grass formations, in part; SCHNEIDER (**21**), gravel slide and half gravel slide formations, in part.

The principal herbaceous growth of dry coarse-soil situations in the foothills presents very great variability, and is very generally distributed, occupying not only large areas by itself, but occurring in mixture with shrubs and trees representing different associations. It is perhaps not too much to say that only a small proportion of

the area in which the rock pine is of frequent occurrence is occupied by actual forest; the usual vegetation of the pine-sprinkled upland is open, the ground-cover is made up of associations of herbaceous plants or low shrubs; prominent among these is the primitive grassland. It enters largely into the ground-cover of other mixed associations also, in which trees and shrubs other than rock pine are conspicuous. The variability of such an open ground-cover as the primitive grassland is so great that no particular set of plants can be said to characterize the whole community, although certain features are common to all of its variants or consocies: (1) they constitute the first vegetation in new and unfavorable habitats; (2) this vegetation is sparse and open; (3) it is made up of an assemblage of species typical of coarse soils and rather considerable exposure to sun and wind, some more commonly in the plains, others in the mountain region (many of these plants are common to several of the consocies, though some few are typical only in the more extreme developments of particular consocies-habitats, as *Erigeron compositus* in packed granite-gravel); (4) as development of vegetation proceeds in the several consocies, with accumulation of the plant remains, closing of the plant cover, etc., they resemble one another more closely, converging into a less open growth, which may be known as the foothills dry grassland association, the next higher in the genetic series. Many of the species of the primitive grassland seem not to be particularly xerophytic, as *Thlaspi coloradense* and *Gilia aggregata*, for these are active during the early part of the season, when the moisture supply is ample. Such plants are very widely distributed in the foothills and are not characteristic of particular habitats nor of the species groupings of particular plant communities.

A partial list of species of the primitive grassland follows:

SPECIES LIST: PRIMITIVE GRASSLAND

Selaginella densa (*l*)
Aristida longiseta (*l*)
Stipa comata (*l*)
Bouteloua hirsuta (*l*)
Koeleria cristata (*ch*)
Sitanion brevifolium (*l*)
Phlox multiflora
Gilia aggregata
Gilia pinnatifida
Phacelia heterophylla (*ch*)
Oreocarya virgata
Pentstemon humilis

Arenaria Fendleri
Paronychia Jamesii (*ch*)
Berberis aquifolium
Thlaspi coloradense
Physaria floribunda (*l*)
Lesquerella montana
Sedum stenopetalum (*ch*)
Potentilla pennsylvanica strigosa
Potentilla Hippiana
Astragalus Purshii
Geranium Parryi (*ch*)
Mentzelia spp.
Chrysopsis villosa (*ch*)
Chrysopsis spp. (*ch*)
Townsendia exscapa
Townsendia grandiflora
Machaeranthera aspera
Helianthus pumilus
Hymenoxys floribunda (south)
Gaillardia aristata
Artemisia frigida (*ch*)
Artemisia gnaphalodes var. (*ch*)[3]
Senecio Nelsonii (*ch*)

The more important representations of the association in special habitats:

(1) The mixed consocies of mixed detrital slopes. This term may be applied to the very sparse plant community of slopes on which the fragments of rock-débris are of all sizes, and in which as a result conditions for plant life vary extremely locally. The vegetation may be regarded as a mosaic of different variants of primitive grassland, with the addition of certain components from other vegetation types, as the lichen, shrub, and pine associations (see figs. 4, 8).

(2) The *Geranium-Chrysopsis* consocies of unstable granite-gravel slopes, in which the loose bunches of these two plants are the most frequent or the only plants in the loose decomposed granite soil.

(3) The *Artemisia frigida-Koeleria* consocies of stony detrital slopes (rock talus, frequently). The habitat is quite common though seldom very extensive; the sage may be very abundant without the grass *Koeleria;* it is an important species in the northern Great Plains and in the mountains up to 10,000 ft.

(4) The compacted granite-gravel consocies. Dwarfed plants of *Erigeron compositus*, *Senecio Nelsonii*, and a few other species are characteristic in level or gently rolling top surfaces, on which the thin coarse soil has become compacted into a hard floor (fig. 3). In its most extreme condition seen, the *Erigeron* was the only plant, occupying less than 4 per cent of surface. Rather infrequently, *Potentilla Hippiana* occupies these situations, forming a pure growth which spreads vegetatively.

(5) The mat consocies of gravel slides. These habitats are more frequent in the Pike's Peak highland than in the Front Range proper, where they are

[3] This plant has narrow pinnately 5-divided leaves, and appears to be quite constantly different from the entire or apically 3-divided form with dense white canescence. With this structural difference is an apparently constant habitat difference; the dissected form is usually in very coarse soil, the other in clay, abundant only at the mountain-front. It is hoped that experiments can be made on these to determine whether the forms are genetically distinct, as they are ecologically.

best developed on south-facing slopes, commonly at the bottoms of open canyons, beside graded roadways. Species of *Gilia*, *Physaria*, *Phacelia*, *Berberis*, *Gaillardia*, and *Pachylophus* are characteristic. Gravel slides have been studied by CLEMENTS, and by SCHNEIDER (**21**).

The primitive grassland is closely related to certain associations of the Plains region, notably the mat association (**9,** p. 376; **24,** p. 393), and the *Gutierrezia-Artemisia* association (**24,** p. 398), and to the other primitive assemblages leading to short-grass. It is more generally distributed, as would be expected, at lower elevations

FIG. 3.—Granite-gravel floor, with much bare surface, some primitive grassland, and mats of *Arctostaphylos;* in background rocky summit or knob, with scattered pines; Flagstaff Mountain.

and more southerly parts of the mountain region, and in the more exposed habitats. It probably occupies a larger proportion of the total area in the lower parts of the Front Range than any of the other associations in their unmixed condition.

ROCK PINE ASSOCIATION

CLEMENTS (**1**); RAMALEY (**10, 12, 14**); ROBBINS and DODDS (**18**), distribution of conifers on the mesas near Boulder; SHANTZ (**22,** p. 184); WATSON (**25,** p. 207); YOUNG (**28,** p. 337).

Pinus scopulorum, variously called the rock, western yellow, or bull pine, is the important tree in the foothills. Its plasticity

is remarkable, growing in all kinds of soil, on slopes of every angle and every direction, through wide variations in soil moisture, evaporation, light, and temperature. Its wide geographic and altitudinal range is an expression of this plasticity. In favorable situations it grows rapidly, with straight trunk and branches regularly arranged; in the more exposed places it is reduced in size, and commonly gnarled and irregular. Distribution of the pines is largely a matter of establishment, since the critical stages are seed burial, germination, and the young seedling period. Crevices and soil-filled spaces between rocks, usually of small area, afford lodging places for the seeds; exposed summits and slopes of fine soil are mostly covered with grassland. Small areas of soil deposition may allow burial of many seeds, and consequent development of dense young stands. Seeds germinate well in the tangled mats of *Ceanothus Fendleri* (see under *Ceanothus* association). The first few years of the seedling are safely passed only when several favorable seasons are successive (at least in exposed situations), as shown by RAMALEY (13, p. 30) for the high mesas near Boulder.

According as establishment is abundant or very sparse in a given station, the growth is closed, giving a true pine forest, or scattered, resulting in the well known open or parklike appearance; this is a mixed vegetation of which the pines form only one component. They may later dominate the whole area if new pines can germinate beneath, but on the whole the closed pine forest is relatively infrequent. Just how important an influence in the foothills fire has been, and is, is very difficult to determine; it is said by some residents that the whole region just north of Boulder Creek was once much more extensively forested than now; but if fire is of fairly frequent occurrence in a region, it is an environmental factor to be taken into account. Its effect is wholly favorable to the grasslands and primitive growths, at the expense of the pines (fig. 4).

In the lower and more southerly parts of the foothills, dry grassland and particularly primitive grassland form the ground cover in most areas of scattered pines. The spiny shrub *Ceanothus Fendleri* is also commonly seen between the trees. Away from the individual trees, and often even at their very bases, the plant cover is mostly not different from its condition where

there are no pines. The trees frequently do modify conditions of growth for ground plants, however, where pine needles accumulate, but this effect is very local. Farther up, and to the north, and apparently more closely associated with pine growths, the bearberry (see under *Arctostaphylos* association) is an important part of the ground-cover between scattered trees.

Juniperus scopulorum is an infrequent though locally conspicuous tree species found with the pines. *Pseudotsuga mucronata* also mixes in to some extent, even in a few fairly xerophytic stations. *Juniperus communis sibirica* is a ground shrub of infrequent occurrence. *Pinus flexilis* is very locally represented, although not confined to the foothills. *Pinus Murrayana*, the

FIG. 4.—Shallow ravine head; mostly grassland, with fine soil at bottom, and thinner and rockier soil on side-slopes; in coarse soil are numerous pines and *Arctostaphylos* (foreground); in middle ground a considerable clump of *Prunus demissa* (leafless condition), occupying soil moist from seepage; April 1914.

lodgepole pine, of the montane zone, mixes with the rock pine in the upper foothills. The rock pine is by no means absent from the montane zone, and is even quite abundant there if the lodgepole is absent, as in the Pike's Peak highland generally.

The pine association in its unmixed form (practically closed forest) has very few open spaces. Natural pruning of the lower branches is general. Old needles strew the ground; the light is much reduced; the two influences, mulch and shade, acting together or singly, exclude practically all ground plants from the closest stands, and all but a few from less dense forests. Plants of primitive grassland very seldom persist in shade. Relics of former vegetation are seen in less advanced stages, including occasional plants of *Opuntia*, *Cercocarpus*,

bunch-grasses, and others. A few species commonly found in the undergrowth of unmixed but not densely shaded forest are *Harbouria trachypleura*, *Aletes acaulis*, *Senecio* (one or two spp.), *Solidago* (several spp.), and *Pentstemon humilis*.

PINYON-CEDAR ASSOCIATION

CLEMENTS (**1**, p. 8), foothill woodland formation; SHANTZ (**22**, p. 184); WATSON (**25**, pp. 205–207), cedar and pinyon formations.

The pinyon, or nut pine, *Pinus edulis*, and less abundantly the cedar of the southern Rockies, *Juniperus monosperma*, are conspicuous plants in the mountain-front of the southern part of the state and in the adjoining foothills. Toward the south conditions are generally more xerophytic at the mountain-front; there the rock pines are common only in higher elevations; they are replaced below by the pinyon. Like the rock pines farther north, the pinyons show local extension eastward into the plains, in rocky habitats, such as the canyon-walls of rock outcrops, and the bluff-crests of the plains stream valleys.

Between the trees are plains or semi-desert plants, many southerly species being present which are rare or absent farther north than about Colorado Springs. One of the most notable of these is the candlestick cactus, *Opuntia arborescens*, common at the mountain-front on rock-strewn slopes and mesas.

The pinyons (and to a smaller extent the cedars) are typically broadly rounded, the diameter of the crown being usually as great as the height of the tree, which is rarely more than 12–15 ft. The trees are usually separated so that the crowns are distant from each other by a diameter or a little less, in the closer stands. The writer has never seen a really closed pinyon forest in which the crowns would form a continuous canopy. The interval between trees increases with xerophytism and exposure, and the branches are less symmetrically developed. Where the habitat is extensive, the pinyons are quite uniformly dotted over the general area. On rocky ridges and mesa-crests the trees are in ragged lines, in small clumps, or irregularly scattered.

QUERCUS ASSOCIATION

CLEMENTS (**1**, p. 6) and SHANTZ (**22**, p. 179), foothill thicket formation, in part; WATSON (**25**, pp. 207–210), white oaks in the yellow pine association.

East of the range-crest oaks may be seen nearly as far north as Denver; however, they form more extensive growths to the southward. North of the Platte-Arkansas divide they are perhaps more abundant at the mountain-front and in the Plum and Cherry Creek

valleys than in the foothills proper; they range into finer soils than do the pines. In the foothills as well as at the mountain-front the oaks may share mixed rocky slopes with local representations of *Cercocarpus*, pinyon, rock pine, or grassland associations, or may alternate with them. The extent to which they replace the rock pine on south-facing foothill slopes is appreciable even north of Perry Park, and is increasingly considerable southward. There is no apparent reason why they would not grow north of their

FIG. 5.—Alternation of mixed grassland and oak forest, west of Castle Rock, July 1913; tall herbs conspicuous at border.

present limits in the mountain-front; some of them extend north on the west side of the range-crest even into Wyoming (fig. 5).

The taxonomic condition of these oaks is one of confusion. RYDBERG'S *Flora of Colorado* (19) lists 11 species, all occurring at or near the eastern mountain-front. *Quercus Fendleri* appears to be distinct, much more xerophytic, more southerly in distribution. The intergradations with most of the others are such that specific determinations are very difficult. CLEMENTS mentions *Quercus Gunnisonii* as the chief species of the Manitou vicinity. Certain Colorado botanists now speak of the doubtful oaks collectively, for the present, simply as *Quercus* spp. The writer has thus far not been able to distinguish different habitat groups within these *Quercus* spp. (cf. SHANTZ, 22, p. 179).

So many of the oaks do not reach tree size that the assemblage in many places presents the appearance of chaparral. As might be expected from their wide range of habitat-tolerance, they vary considerably in appearance, from shrubby scattered trees or stunted thickets, to low forest with mesophytic undergrowth. In very favorable stations, as along streams in the southern foothills, the oaks may reach a height of 20 ft. and more. The undergrowth in ungrazed parts of the oak scrub has a decidedly mesophytic stamp during the moister part of the season; *Pulsatilla*, *Castilleja*, *Monarda*, *Calochortus*, *Lupinus*, *Geranium*, *Galium boreale*, *Campanula*, *Thermopsis*, *Danthonia*, *Pentstemon unilateralis*, are typical of oak borders and less densely shaded parts within. Dense closed shaded oak scrub shows abundance of a tall white-flowered umbellifer, *Ligusticum Porteri* (?).[4] Late summer shows many of the less xerophytic composites, including species of *Aster*, *Solidago*, *Erigeron*, and *Brickellia grandiflora* var. *minor*. The undisturbed clumps of small oak trees, where these alternate with dry grassland, are often bordered with tall, rather mesophytic herbs, as *Lupinus argenteus*, *Monarda* spp., and *Achillea millefolium* L. (*A. lanulosa* Nutt.), as may be seen in fig. 5, taken west of Castle Rock.

Low scrubby oak thickets, in grazed areas, are mostly impenetrable to horses and cattle; they are, however, eaten from the outside, and the patches thus slowly reduced in area. This results in a complete replacement of oak by grassland, as stated by SHANTZ (**22**, pp. 182, 203). When, however, the height of the small trunks in the middle of a clump becomes too great for the animals to reach the top leaves, their safety is assured. In these taller growths the lower parts of the trees are much less dense; if there is no outer border of dense thicket, grazing animals are enabled to enter; the assemblage is now a scrubby forest of low trees, with open spaces between the trunks and very scanty undergrowth, as in fig. 6. Grazing animals may thus have a large part in determining the character and distribution of the oak vegetation.

CERCOCARPUS ASSOCIATION

CLEMENTS (**1**, p. 6) and SHANTZ (**22**, p. 179), foothill thicket formation, in part; RAMALEY (**12**, pp. 124–126), *Cercocarpus* shrub formation; RAMALEY and ROBBINS (**15**), local distribution in a square mile of rock ridge and foothills; SCHNEIDER (**21**, p. 292), thicket of south slopes, in part.

Ragged shrubs of *Cercocarpus parvifolius*, or, as it is called, mountain mahogany, form a characteristic vegetation in dry exposed rocky places, particularly along the mountain-front, on butte-slopes, hogback ridges, stony mesa-crests; in the foothills it is most abundant on south-facing side-slopes, or on the outermost slopes facing eastward on the plains. The stony fragments of the

[4] Either *L. Porteri* C. and R., or *L. affine* A. Nels., as determined by E. E. SHERFF.

soil vary from those of coarse granite-gravel to the variously sized blocks of rock talus.

The shrubs are 2–5 ft. high, very loose in habit, with few branches and reduced leaf surface. The fruits are provided with long plumed awns. The plants are separated, being regularly spaced like the pinyons, the intervals likewise varying with degree of exposure. The habitat relations of *Cercocarpus* are in fact quite like those of the pinyon, and it is north of the pinyon area that the mountain mahogany association is best developed. The interspaces

FIG. 6.—Open grove aspect of oak assemblage, caused by entrance of grazing animals, Perry Park; open mixed grassland in coarse soil occupies foreground.

between plants may be almost bare, or may be occupied by a sparse growth of xerophytes, most of them plains plants or representatives of the primitive grassland, the mat growth-form being common.

ARCTOSTAPHYLOS ASSOCIATION

COWLES (**3**, p. 367) and GATES (**6**, p. 306), Lake Michigan dunes; WHITFORD (**26**, p. 298), northern Michigan. In the Colorado foothills: ROBBINS (**16**, p. 44); SCHNEIDER (**21**, p. 299); SHANTZ (**22**, p. 186).

The *Arctostaphylos-Juniperus* association of the northeastern coniferous forest region is very well known to students of vegetation. Practically the same community is represented in the Rocky Mountains, associated there as elsewhere with coniferous vegetation. The same plant species and the same creeping habit are seen. The

important difference, as seen in the Front Range foothills, is that the juniper is very infrequently seen, the *Arctostaphylos* mostly dominating alone.

Conditions of soil-moisture, soil-texture, position, slope, and exposure are varied. The creeping mats of bearberry are seen on rock, in gravelly decomposed granite, and in fine moist humous soil; on practically all slopes, shaded and sunny, and through a considerable range in altitude. The growth is more extensive and more frequent, however, away from the mountain-front, at elevations 800–1200 ft. above the lower limit of rock pine, being increasingly abundant from that height upward, and being perhaps more typical of montane than of foothills vegetation. Its most frequent habitat in the foothills is the rolling floor of the granitic upland, the soil of which is thin, coarse, mostly compacted (granite-gravel). Here the conspicuous vegetation is rock pine, in open array of scattered clumps and single trees. Parts of the treeless surface are occupied by large mats of *Arctostaphylos*, with admixture of *Ceanothus Fendleri* (less of this upward); the rest of the area is bare or nearly so, with a few scattered herbaceous plants, mostly of primitive grassland.

CEANOTHUS ASSOCIATION

ROBBINS (16, p. 41); WATSON (25, p. 207).

The spiny shrub, *Ceanothus Fendleri*, is ecologically similar to *Arctostaphylos* in many respects. It forms a low, matlike, spreading ground cover, and occurs to some extent in mixture with bearberry mats. It differs from the other in being typical of more exposed and xerophytic slopes, in being abundant at lower altitudes, and more southerly in geographic distribution. MILLARD S. MARKLE informs the writer that the *Ceanothus* community is important in the Sandia Mountains of New Mexico, occurring frequently with the oaks and with *Robinia neo-mexicana*. *Ceanothus* ranges into dry fine-soiled habitats more frequently than *Arctostaphylos*, and is closely associated with grassland, rather than pine forest. It is not evergreen.

Ceanothus shrubs occur in closely set or scattered patches, mostly in unstable gravelly or finer soil of detrital slopes. They have a strongly accelerative part in vegetation-development. Their numerous twigs and thorns, even in the leafless winter condition, catch and hold wind-blown and washed-down soil particles and bits of plant débris, thus stabilizing and adding to the soil, and accumulating humus. In one station this had even resulted in the building of small dunes of wind-blown dust, of about 8 inches height and 18 inches diameter. Seed burial is favored in these mats, as well as germination. Some of the more mesophytic of the foothills plants are seen growing up through the tangled branches; pine seedlings also germinate in the shelter of *Ceanothus*, which may thus be an important factor in reforestation. On dry, burnt slopes *Ceanothus* frequently covers a considerable proportion of surface and, with the *Rhus cismontana* shrub growth, is an important stage in succession after burns.

Ceanothus mollissimus and what appears to be *Ceanothus subsericeus* Rydb. occasionally occur with the spiny species, in the less xerophytic stations. *Ceanothus velutinus* is rare in the lower foothills, but is frequent at higher elevations and farther north. Herbs of the primitive grassland and mixed grassland commonly grow out from between the twigs of *Ceanothus Fendleri*, and to some extent are seen in the spaces between the mats.

FOOTHILLS MIXED GRASSLAND ASSOCIATION

CLEMENTS (1), ground-cover in the foothill thicket and pine formations, in part; RAMALEY (12), foothill sagebrush-grass formation; SCHNEIDER (21), half gravel slide formation, and grassland of north slopes; SHANTZ (22), *Bouteloua* formation, in part: its modified form at the mountain-front; VESTAL (24, p. 386), *Bouteloua* mixed consocies, as developed at the mountain-front; WATSON (25, pp. 209, 210), herbaceous ground-cover in the yellow pine association, and mountain "meadows."

The mixed grassland association normally develops from primitive grassland, one of its important features being the establishment of the dominant *Bouteloua oligostachya*, the grama grass of the plains. It thus differs from the primitive grassland in that (1) the ground cover is less open, though still generally xerophytic; (2) the soil is usually more stable (in most situations a physical cause, rather than the effect, of the more permanent vegetation); (3) the soil is more finely broken up, and to it may be added considerable humus; and (4) a number of plains, prairie, and foothill species absent or rare in the primitive grassland are established.

The assemblage is most heterogeneous, since the many plants include widely diverse ecological, geographic, and floristic types. Extreme xerophytes and relatively mesophytic plants, plants of widely varying growth-form and seasonal relations, of great difference in plasticity to environmental variation, in altitudinal and habitat range, may occur in the same small grassland area. This mixed vegetation is really very closely allied to the modified plains grassland mentioned as the *Bouteloua* mixed consocies of the short-grass association (24, p. 386). This is found in the mixed mesa soils of the mountain-front zone just outside the foothills. The conditions which would result in heterogeneity of the grassland vegetation are probably similar in the lower foothills to those of the mountain-front; some of these are given in the article cited (24, pp. 381, 382).

So many species occur regularly in the mixed grassland, and the variability in floristic composition in particular stations is so great, that a selected list of plants equally representative of various localities and habitats cannot be

given. By way of illustration, however, a list of the plants observed in a particular mixed grassland station may be presented, and this is followed by a list of some other species commonly found in the community, but which happen to have been absent from the station selected. The station is on the east slope, not far from the top, of a hill a little over two miles west of the mountain-front and a little north of Boulder, in section 36, T 2 N, R 72 W. The hill is marked in the Boulder quadrangle of the United States topographic atlas by the altitude of its summit, 7168 ft. The spot studied most in detail is at about 7000 ft.; exposure is considerable, as the slope is even and treeless; drainage is probably quite rapid; the soil coarse, with but little humus; proportion of bare surface about 15 per cent on June 18, when the list was made. All of the plants marked as abundant or frequent occur in practically every square meter of surface.

PLANT COMPOSITION OF A TYPICAL MIXED GRASSLAND STATION

Bouteloua oligostachya (*a*)
Phacelia heterophylla (*a*)
Chrysopsis villosa (?) (*a*)
Senecio oblanceolatus (*a*)
Geranium Parryi (*a*)
Artemisia frigida (*a*)
Aragallus Lambertii (*a*)
Koeleria cristata (*f*)
Lesquerella montana (*f*)
Mertensia lanceolata (*f*)
Linum Lewisii (*f*)
Carex pennsylvanica (*f*)
Gilia pinnatifida (*lf*)
Gilia spicata (*lf*)
Helianthus pumilus (*lf*)
Cerastium arvense (*lf*)
Aragallus albiflorus (*lf*)
Stipa comata (*lf*)
Eriogonum umbellatum (*i*)
Opuntia polyacantha (*i*)
Oreocarya virgata (*i*)
Artemisia gnaphalodes var. (*i*)
Astragalus flexuosus (*i*)
Eriocoma cuspidata (*i*)
Mamillaria vivipara (*i*)
Sitanion brevifolium (*i*)
Gaillardia aristata (*i*)
Phlox multiflora (*i*)
Potentilla pennsylvanica strigosa (*i*)
Euphorbia robusta (*i*)
Aletes acaulis (*i*)
Poa longipedunculata (*i*)
Eriogonum alatum (*i*)
Townsendia exscapa (*i*)
Townsendia grandiflora (*i*)
Allium sp. (*i*)

The order in which the species are listed gives a rough approximation of their relative importance as making up a part of the vegetation, in descending scale. The names of plant species elsewhere frequent in the association follow:

ADDITIONAL SPECIES FREQUENT IN MIXED GRASSLAND

Woodsia oregana
Selaginella, two spp.
Aristida longiseta
Muhlenbergia gracillima
Poa crocata
Echinocereus viridiflorus
Gaura coccinea
Cymopterus acaulis
Gilia aggregata et spp.
Lithospermum multiflorum

Poa Fendleriana
Agropyron Smithii
Elymus triticoides
Leucocrinum montanum
Calochortus Gunnisonii
Yucca glauca
Zygadenus intermedius
Comandra pallida
Allionia linearis et spp.
Pulsatilla hirsutissima
Argemone intermedia
Corydalis aurea
Draba spp.
Erysimum asperum
Potentilla spp.
Astragalus spp.
Psoralea tenuiflora
Malvastrum coccineum
Viola Nuttallii
Mentzelia spp.
Onosmodium occidentale
Pentstemon humilis et spp.
Castilleja integra et spp.
Campanula rotundifolia
Liatris punctata
Grindelia squarrosa
Chrysopsis spp.
Solidago spp.
Aster spp.
Machaeranthera aspera et spp.
Erigeron spp.
Ratibida columnaris
Helianthus spp.
Hymenopappus filifolius
Hymenoxys floribunda
Artemisia aromatica
Artemisia canadensis
Senecio plattensis et spp.
Senecio spartioides
Nothocalais cuspidata

As regards distribution of the mixed grassland association in the foothills, it may be said that the primitive grassland is more frequent and occupies areas of greater extent, because of the general instability and rocky character of the sloping surfaces. In the upper foothills mixed grassland is absent from compacted soil level or rolling surfaces generally occupied by pine and *Arctostaphylos*, etc., but dominates on the more exposed mountain sides, which are treeless. The mixed grassland, like primitive grassland, is subject to a gradual ecological and floristic variation, from the south northward, and from the short-grass of the plains to the montane dry grassland of elevations from 8500 to 10,000 ft.

BUNCH-GRASS ASSOCIATION

CLEMENTS (1, p. 6), *Andropogon*, etc.; SCHNEIDER (21), half gravel slide formation, in part; SHANTZ (22, p. 43), *Bouteloua hirsuta* consocies. with *Andropogon* spp., *Atheropogon*, etc.; VESTAL (24, pp. 388–390), bunch-grass association: photograph and citation to descriptions in other regions; WATSON (25, p. 209), *Andropogon*, etc.

The bunch-grass vegetation of the foothills is quite similar to that of the mountain-front and over the whole prairie region, including most of the same species, but containing in addition other grasses of similar growth-form but of different geographic distribution. With the bunch-grasses are many composites and other

plants of the mixed grassland, such as *Liatris*, *Chrysopsis*, *Eriogonum alatum*, etc. The tufted bunch-grass growth-form is well known; the roots are deep and numerous; the plants are mostly late in flowering; they are active during the whole growing season, depending on a constant moisture supply. The chief habitats in the foothills which satisfy this condition are rocky or very coarse gravelly slopes, exposed and dry at the surface, but with rather more moisture beneath than in most areas of mixed grassland; these situations are consequently rather locally developed only.

PRAIRIE BUNCH-GRASSES OCCURRING IN FOOTHILLS

Andropogon scoparius (*a*)
Andropogon furcatus (*a*)
Hilaria Jamesii (*li*)
Sorghastrum nutans (*lf*)
Muhlenbergia gracilis (*f*)
Sporobolus heterolepis (*lf*)
Atheropogon curtipendulus (*f*)
Koeleria cristata (*f*)

OTHER FOOTHILLS PLANTS OF BUNCH-GRASS TYPE

Trisetum montanum (*l*)
Festuca confinis (*l*)
Agropyron occidentale (*l*)
Agropyron spicatum
Sitanion longifolium
(?)Elymus triticoides

Hilaria is a southern plant and has not been seen north of about Canyon City. *Sorghastrum* and *Hilaria* appear not to extend far into the foothills. *Koeleria* ranges into many widely varying habitats and is found with many different plant assemblages. This may partly be due to its early ripening (it flowers in June), which may allow it to escape the dryness of the latter part of the season. Most of the plants of the second group bloom in early summer also; they are frequently found in clumps of one species, in rock crevices or coarse soils. *Trisetum* ranges into the montane zone, but not into the plains; it is restricted to moister places than most of the others. *Agropyron spicatum* is one of the chief dominants of the extensive grassland areas in the northwestern states, in intermontane valleys and the Columbia Basin plains. It too matures early in summer and is dried up the rest of the season. *Elymus triticoides* is included with some hesitation; it may be more like the grasses of the primitive bunch-grass type (**24**, p. 397).

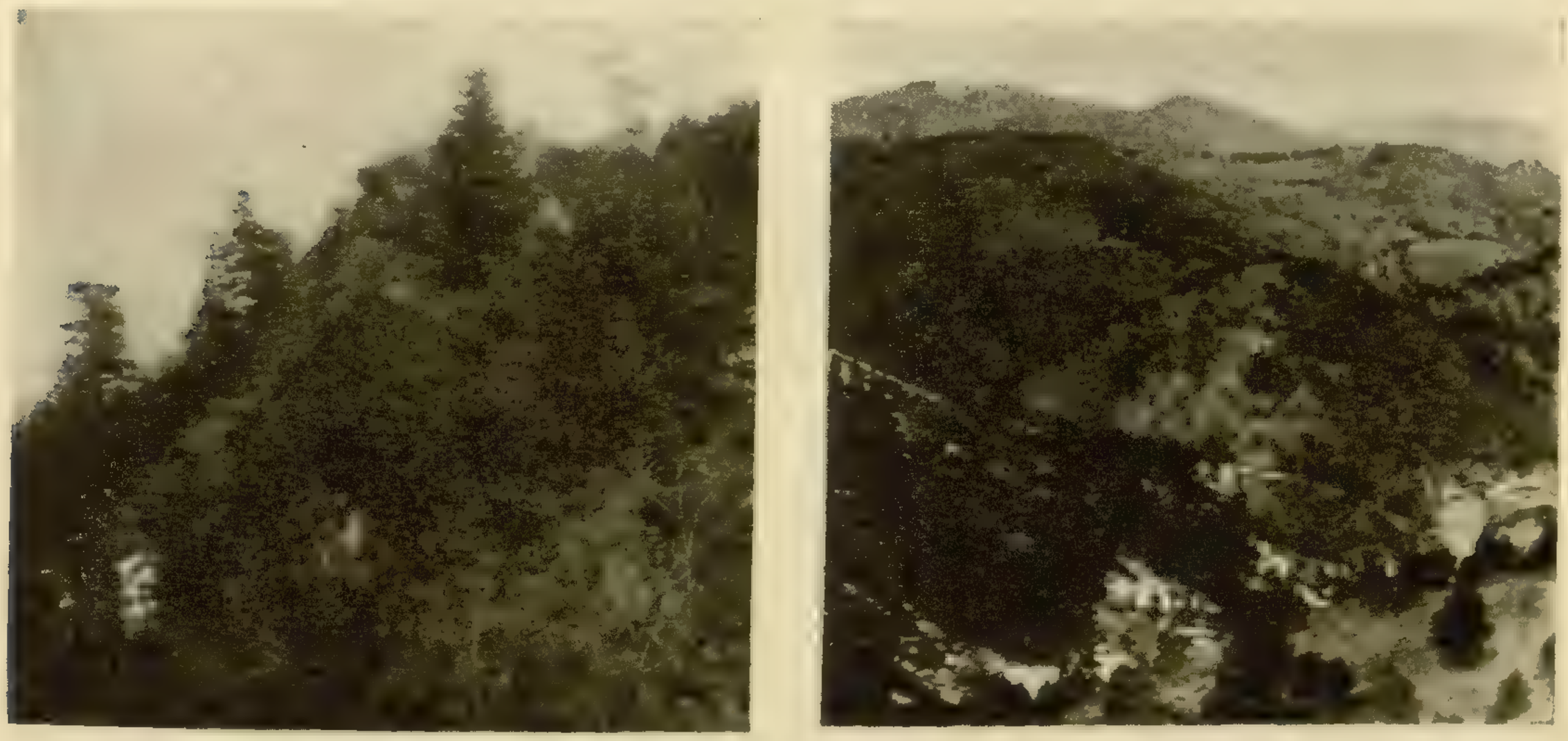
PSEUDOTSUGA ASSOCIATION

CLEMENTS (**1**, p. 14); SCHNEIDER (**21**, pp. 299, 300), with list of herbaceous plants; RAMALEY (**14**, pp. 251, 262); WATSON (**25**, p. 211); YOUNG (**28**, p. 343).

The Douglas "spruce," *Pseudotsuga mucronata*, is, like the rock pine, one of the most abundant and widely distributed conifers of

western North America, but in the foothills of the Front Range in Colorado it is relatively very local in occurrence. It is frequent only on north-facing slopes and in canyons, where the snow lies deep and late. It grows in close stands or as scattered trees (fig. 7).

Small trees of *Juniperus scopulorum* may occur infrequently in the *Pseudotsuga* forest; in unshaded areas with moist soil a few aspens may be found. *Arctostaphylos* and the prostrate *Juniperus communis sibirica*, so frequently associated with it, are seen as relics. The moist and sheltered slopes on which *Pseudotsuga* grows may in its stead be covered by the mesophytic grassland association, and many of its plants occur scattered among the conifers, such as



FIGS. 7, 8.—Fig. 7, *Pseudotsuga* association on a north slope; fig. 8, another general view, showing prevalence of grassland on side-slopes; trees conspicuous in profiles of distant slopes.

Mertensia spp., *Campanula rotundifolia*, *Pulsatilla hirsutissima*, *Saxifraga rhomboidea*, *Aster laevis*, and one or two small ferns.

The rock pine grows well in the moist habitats of the *Pseudotsuga*, if the young trees can get a start, and so the two species are commonly found in mixture, especially toward the top of canyon-slopes and in other less protected places. Also *Pseudotsuga* can range into the habitats of the pine, where, however, it is usually of less symmetrically spire-shaped form, and with fewer and uneven branches, so that the growth habit resembles that of the pine.

POPULIS-SALIX STREAM-SIDE ASSOCIATION

RAMALEY (12, p. 127, 14), part of the canyon forest formation; WATSON (25, p. 21), *Populus angustifolia* society; YOUNG (28, pp. 330–336).

The poplars and willows of stream-sides form a nearly continuous belt in the wider and more open canyon-bottoms of the foothills. *Populus angustifolia*,

the narrow-leaved cottonwood, is the largest and most frequent species. The willows include *Salix irrorata* and *S. exiguus*, forming shrubby clumps; and *S. Bebbiana*, *S. amygdaloides*, and *S. lasiandra*, small trees. The hackberry, *Celtis reticulata*, is perhaps more typically found scattered along stream-sides in quite exposed places than with other trees. It is also common in such habitats in New Mexico. Certain plants common in the canyon forest are also quite characteristic, in the rather less exposed stream-side situations, replacing the cottonwoods and willows in small areas, or intermingling with them. Such plants are *Alnus tenuifolia*, *Betula fontinalis*, *Acer Negundo*, and the shrubby *Cornus stolonifera*. Scattered plants of the mixed shrub association are also frequently seen: *Bossekia*, *Ribes*, *Rosa*, *Crataegus*, *Prunus demissa*, and others.

CANYON FOREST ASSOCIATION

RAMALEY (**12**, p. 127); YOUNG (**28**, pp. 333, 335), *Alnus-Betula-Corylus* assemblage; (*l.c.*, p. 334), *Crataegus* assemblage, etc.; DANIELS (**4**, pp. 21, 27).

The canyon forest, which contains many of the deciduous tree species of the foothills, is typically developed in local mesophytic stations, such as the slopes and bottoms of narrow canyons, in which the soil is moist (usually from seepage), and the air comparatively humid, due to the shade and the shelter from wind. A selected list of species is here given:

PLANTS OF FOOTHILLS CANYON FOREST ASSOCIATION

Trees

Alnus tenuifolia
Betula fontinalis
Salix Bebbiana (*i*)
Populus tremuloides (*li*)
Amelanchier alnifolią (*li*)
Prunus pennsylvanica (*ch*)
Prunus americana
Prunus demissa (Nutt.) Dietr.[5] (*ch*)
Robinia neomexicana (*l*)
Acer glabrum (*ch*)
Acer Negundo (*l*)
Crataegus coloradensis et spp.

Shrubs

Corylus rostrata (*l*)
Ribes longiflorum
Physocarpus Ramaleyi (*i*)
Rosa Sayi et spp.
Rhus Rydbergii (*i*)
Vitis vulpina (*l*)
Parthenocissus vitacea (*l*)
Viburnum pauciflorum (*li*)

[5] JONES (**8**, p. 35) fails "to see any ground for NELSON'S *P. melanocarpa*, even though NUTTALL describes his as red-fruited, for we know that this species has fruit red till dead ripe, when it turns black."

Herbs

Pteridium aquilinum	Fragaria pauciflora et spp.
Smilacina stellata (*ch*)	Aralia nudicaulis
Smilacina amplexicaulis (*ch*)	Viola canadensis Rydbergii (*ch*)
Stellaria Jamesiana	Castilleja miniata et spp.
Thalictrum spp.	Monarda Ramaleyi et spp.
Aquilegia coloradensis	Hydrophyllum Fendleri (*ch*)
Delphinium Nelsonii (*ch*)	Galium boreale (*ch*)
Ligusticum Porteri (?)	Galium aparine
Saxifraga rhomboidea (*ch*)	Galium Vaillantii

The canyon forest presents a wide range of variability, according as favorable ground conditions are uniform or interrupted; thus in rocky canyon-bottoms and slopes it is patchy in development. It may merge into, or mingle with, areas of *Pseudotsuga*, mixed shrub, aspen, *Populus-Salix*, *Quercus*, and moist grassland growths. The herbs especially may be no more typical of unmixed mesophytic deciduous forest than of many other mesophytic habitats. The characteristic plants growing in the shade of large shrubs and trees are *Viola*, *Hydrophyllum*, and one or more species of *Galium*. These are abundant in unmixed canyon forest, at least in the northern foothills.

Amelanchier is an important component only in the upper foothills and the montane zone, or farther north and west in the Rocky Mountains. *Acer glabrum* often occurs by itself on north or shaded slopes, the bushy plants 10–15 ft. in height, and in most places considerably separated. *Prunus demissa*, and several species of *Crataegus* (mostly *C. coloradensis* and *C. cerronis*), together or singly, dominate tall thickets or low forests, which may be regarded as transitional between the mixed shrub and canyon forest associations. In new growths or exposed situations they are low and scrubby; in other places they form a taller and closed growth, with a lower stratum of mesophytic herbs, and may properly be spoken of as forest. *Prunus demissa* and *Crataegus* form relatively much more extensive areas of vegetation in the northern foothills and especially along the northern mountain-front than in the southern part of Colorado. *Robinia* is abundant in the southern third of the foothills area. It ranges into drier habitats, in which it is low and scrubby.

The *Alnus-Betula* consocies has been mentioned as being abundant along mesophytic stream-sides. *Corylus* is frequent only in such situations, occurring in places alone, in others with *Alnus* and *Betula*. The climbers, clematis, Virginia creeper, and grape, are local, and more common in sunny openings. *Viburnum* is in moist canyon-bottoms of the higher foothills.

ASPEN ASSOCIATION

RAMALEY (14, p. 251); YOUNG (28, p. 347).

Botanists are familiar with the rôle of *Populus tremuloides* in revegetation of burned areas, and it is prominent in the montane zone in Colorado in this capacity. The general area of the lower foothills, however, is too dry for establishment of aspens, and they occur only locally, in ravines even more mesophytic, perhaps, than the ordinary habitat of the canyon forest. Thus in the Boulder area the stations below 7200 ft. in which aspens have been observed in local abundance are very infrequent. Such stations are usually in sheltered ravines with deep humous soil, abundantly moist. The trees in places are large, the undergrowth very mesophytic, with *Thalictrum*, *Heracleum*, *Castilleja* spp., etc., and particularly *Aquilegia coerulea*. At about 7800 ft. in the same vicinity aspens begin to appear in small clumps on the granite-gravel upland, among more frequent clumps of rock pines. No connection with former fires could here be made out; appearances indicated that perhaps there the aspens might be associated with the moist patches resulting from the tardy disappearance of the deeper snowdrifts of winter. The conspicuous yellow color of the aspens in fall probably tends to exaggerate the popular notion of their frequency of occurrence.

MIXED SHRUB ASSOCIATION

DANIELS (4, p. 20); RAMALEY (12, p. 127), shrubs of the canyon forest; SHANTZ (22, p. 179), thicket formation, in part; notes on distribution and ecological relations of the species; RAMALEY (11); ROBBINS (16); SCHNEIDER (20).

The shrub associations of the foothills, like the deciduous tree growths, are generally found in rocky or coarse soil stations with constant moisture supply in the substratum, which is reached by the deep root systems. Local distribution, as in the case of the pines, is probably restricted by unfavorable conditions for germination over a large part of the general area. It has been observed that, on irregular slopes where the distribution of snow in late spring is uneven, the shrubs occupy the moister spots determined by the deeper snow patches. In deep moist soil it is likely that the shrubs are soon succeeded by trees, as has been observed in some stations. The shrub species most commonly found appear in the following selected list. Certain of the canyon forest plants which occur with the shrubs in the less mesophytic stations without attaining tree size are included here also. It is significant that so many of the

shrubs, and some of the canyon forest plants, have fleshy fruits, and so may be distributed by birds.

PLANTS OF FOOTHILLS MIXED SHRUB ASSOCIATION

Ribes saxosum
Ribes pumilum
Ribes vallicola
Ribes longiflorum (*l*)
Jamesia americana (*l*)
Holodiscus dumosus (*l*)
Physocarpus intermedius (*l*)
Physocarpus monogynus (*l*)
Bossekia deliciosa (*f*, *ch*)
Rubus strigosus (*l*)
Rosa Sayi
Rosa arkansana
Rosa Fendleri
Amelanchier alnifolia (*i*)
Crataegus cerronis
Crataegus coloradensis
Prunus americana (*ch*)
Prunus demissa (*ch*)
Robinia neo-mexicana (*l*)
Rhus trilobata (*ch*)
Ceanothus subsericeus

Amelanchier has been mentioned as being rare in the northern foothills, as may be said also for *Holodiscus*. The common shrubs of rock-crevice habitats are *Jamesia* and *Ribes pumilum*. The yellow-flowered *Ribes longiflorum*, unlike the others of the genus, is more frequent in deep, moist, fine-grained soil than in rocky or coarse soil. *Rubus strigosus* is more common in the upper foothills, and in less exposed habitats. It and the roses are smaller than most of the other shrubs. *Prunus americana* forms low dense thickets in rather exposed places. *Robinia* is southern. *Rhus trilobata* ranges into very xerophytic habitats, and can persist and even establish itself on unstable soil of steep or loose slopes. Although a single species may make up the shrub vegetation at any one spot, numbers of them occur together in a very large variety of combinations, particularly where the habitat is internally diverse. The *Cercocarpus*, *Symphoricarpos*, *Ceanothus Fendleri*, sumac, and bearberry associations, on the other hand, show rather constant differences in environmental relations and distribution from the various representations of the mixed shrub association, and consequently have been separated from it. The relation of the mixed shrub association to the canyon forest has already been mentioned; the two grade into each other, but in the main they are quite distinct.

Where the shrubs grow close together, a mesophytic undergrowth of herbs develops. *Galium aparine* or *G. Vaillantii*, *Delphinium Nelsonii*, and *Viola canadensis Rydbergii* are frequent species. The border of many shrub areas, where there is no grazing, shows tall herbs, as *Lupinus*, *Achillea*, *Monarda*, *Pentstemon unilateralis*, etc. Surface rocks, where present in grassland, may allow the scattering admixture of a shrub element, or even, where the soil is sufficiently moist, invasion of shrubs over the general area.

SYMPHORICARPOS ASSOCIATION

RAMALEY (**12**, pp. 127, 128); ROBBINS (**16**, p. 38).

The *Symphoricarpos* association is best developed in moist, fine-grained soil; best seen, in the foothills, on basal or other deep-soiled detrital slopes, clay or loam, with or without humus. The common species of the Colorado foothills is *Symphoricarpos occidentalis*. The bushes are low, are spaced very close together, and are profusely branched, giving the whole growth a very compact and uniformly dense structure, especially where subject to grazing, as in many stations. From its habitat relations, the bush honeysuckle, as it may be called (it is known in some localities as buckbrush), adjoins a semi-mesophytic grassland in most places, competing and alternating sharply with it. Many of the taller mesophytic herbs are seen at the border, including *Frasera speciosa*, *Thermopsis divaricarpa*, the others already mentioned as bordering canyon forest and mixed shrub, and frequently the tall grass *Stipa viridula*. This border condition is best seen where the *Symphoricarpos* assemblage occupies a depression.

The shrub area is dominated by the one species, although bushes of *Rosa arkansana* are mixed in, abundantly in places, and *Berberis aquifolia* may also be seen. A few herbs may occur underneath.

Symphoricarpos in places forms a border between mixed shrub or canyon forest vegetation and grassland.

MESOPHYTIC GRASSLAND ASSOCIATION

RAMALEY (**12**, p. 129), meadow formation.

There are several kinds of herbaceous vegetation in the foothills, of mesophytic or semi-mesophytic character, which may for convenience be considered together. There is a meadow growth, which shades more or less completely into the western prairie-grass of the mountain-front (**24**, p. 390), on the one hand, and into the forest border and forest undergrowth assemblages on the other. On certain shaded ravine slopes a mixture of mesophytic herbs from several of these assemblages has been observed, apparently independent of any tree canopy. The trees affect the herbs, apparently, mainly or wholly by their modification of physical conditions. A selected list of mesophytic and semi-mesophytic species may be given:

MESOPHYTIC AND SEMI-MESOPHYTIC HERBS OF FOOTHILLS

Stipa viridula (*ch*)
Danthonia Parryi (*f*)
Poa pratensis
Poa Buckleyana
Agropyrum violaceum
Gentiana affinis
Frasera speciosa (*ch*)
Mertensia ciliata
Mertensia lanceolata
Monarda menthaefolia (*ch*)

Calochortus Gunnisonii
Zygadenus intermedius (*ch*)
Iris missouriensis (*li*)
Claytonia virginiana
Cerastium arvense (*ch*)
Delphinium Nelsonii (*ch*)
Thlaspi coloradense (*l*)
Erysimum Wheeleri (*ch*)
Saxifraga rhomboidea (*ch*)
Potentilla pennsylvanica strigosa (*ch*)
Thermopsis divaricarpa (*ch*)
Lupinus argenteus et spp.
Lathyrus leucanthus
Viola canadensis Rydbergii
Pentstemon humilis (*la*)
Pentstemon unilateralis
Castilleja linariaefolia (*ch*)
Castilleja sulphurea
Orthocarpus luteus
Galium boreale (*ch*)
Campanula rotundifolia
Aster laevis
Erigeron flagellaris
Achillea millefolium
Arnica cordifolia
Arnica fulgens (*la*)
Senecio integerrimus (*la*)

The prairie grass aspect has already been mentioned, and a description cited. The foothill meadow assemblage in early summer typically shows such conspicuous plants as *Delphinium*, *Cerastium*, *Arnica*, *Senecio*, and *Castilleja linariaefolia* (*C. sulphurea* is frequent only in the higher elevations). The mixed shrub association frequently alternates with meadow, and encroaches upon it, and is bordered by the taller herbs with that assemblage. The forest border and forest undergrowth communities have also been mentioned.

Moist rock crevices in sheltered ravines become overgrown with cushions of *Selaginella* (fig. 2) and smaller cushions of mosses; humus accumulates by the growth and death of these plants; in this *Saxifraga rhomboidea* and later other herbaceous or woody plants may become established. This is a very common successional series from bare rock in mesophytic habitats.

Herbaceous plants commonly seen scattered along the moist soil of stream margins, in open situations, include *Rumex* sp., *Heracleum lanatum*, *Thermopsis*, and *Lupinus*, with certain grasses, as *Muhlenbergia racemosa*, *Eatonia obtusata*, etc.

Hygrophilous and amphibious plants of the canyon streams may for convenience be mentioned at this point. *Marchantia polymorpha* is found on a very few stream margins on rocks or in crevices in sheltered spots. Many mosses may accompany it, especially where some soil accumulates in cracks of stream-side boulders, etc. *Dodecatheon radicatum* may here be found, or species of *Ranunculus* in boggy places. A number of species are seen in these very restricted boggy places. *Mimulus Langsdorfii* and *Veronica americana* may grow there or in quiet little pools of the stream itself. RAMALEY has given these growths the name Stream Bank Marsh Society (**12, p. 127**).

EASTERN ILLINOIS STATE NORMAL SCHOOL
CHARLESTON, ILL.

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VEGETATION OF HAWAIIAN LAVA FLOWS

VAUGHAN MACCAUGHEY

(WITH TWENTY-TWO FIGURES)

Introduction

This paper is a survey of the more important types of vegetation which occur on the lava fields of the Hawaiian Archipelago and their ecological relations. It has particular reference to the spermatophytes, as our taxonomic knowledge of the native land algae, lichens, bryophytes, and pteridophytes is still in a somewhat fragmentary and unsettled condition. The scope of the paper is further restricted by including only the arid or xerophytic districts where the lava flows are relatively barren. Under humid climate the flows rapidly disintegrate into rich volcanic soil and support a luxuriant rain forest. This paper is concerned with the ecology of the xerophytic regions, as these have largely been neglected in the literature of Hawaiian botany.

There is a widespread association of ideas which couples tropical with humid conditions, due no doubt to the many semipopular accounts of the "tropical jungle" and to the types of vegetation usually exhibited in the northern conservatories. It requires a distinct readjustment of perspective to realize that many tropical regions possess large areas of extreme aridity. The Hawaiian Archipelago, situated just within the tropics in the center of the North Pacific Ocean, admirably illustrates this condition. Most of the popular and semitechnical accounts of the islands have emphasized the beautiful humid woodlands and have either ignored or given scant attention to the vast rocky waste lands of barren lava flow and cinder field.

It has been the writer's privilege, during a residence of 8 years in the islands, to have made many expeditions into these arid regions and to have ascended all of the high mountains of the group. This paper is an outgrowth of these trips, some of which have occupied many weeks. In order to make clear the ecological

background of this lava flow vegetation, it is necessary to sketch briefly the salient features of the Hawaiian volcanic mountains. Detailed accounts may be found in such standard works as those of HITCHCOCK, BRIGHAM, DANA, and DUTTON.

It will be noted that the present paper deals largely with the ecological conditions under which the lava flow vegetation exists. A comprehensive annotated list of the lava flow plants is now appearing in the *Journal of The Linnaean Society*.

Classification of islands

From the standpoint of area occupied by lava flows, cinder fields, and other waste lands resultant from volcanic activity, the islands may be divided into two groups: (1) the lesser islands (Niihau, Kauai, Oahu, Molokai, Lanai, Kahoolawe); and (2) the greater islands (Maui and Hawaii, see figs. 1, 2). The lesser islands are, as a whole, of much greater antiquity than Maui and Hawaii. The erosive agencies have been at work for a much longer time, hence the lava flows have been almost wholly turned into soil. There are some traceable flows still existent on some of the lesser islands, Kauai, Oahu (figs. 3, 4, 5), Molokai, and Lanai, for example, but these are relatively non-consequential as compared with the great stretches of lava covered country on Hawaii and Maui. The lava waste lands, *above the timber line*, on Mauna Loa alone, for example, occupy a greater area than the entire island of Oahu, Kauai, or Molokai. Thus a discussion of the vegetation of the Hawaiian lava flows is naturally restricted chiefly to a consideration of the islands of Maui and Hawaii, the largest and youngest end of the long archipelago. No account is given in this paper of the tiny islands which are strewn over a long axis for 1800 miles to the westward of the larger, inhabited islands. Some of these are volcanic rocks, but the majority are tiny reefs and shoals.[1] Their total area is only 6 sq. miles. All are highly xerophytic.

ISLAND OF HAWAII.—Hawaii, the largest island of the archipelago (4015 sq. miles), is about the size of the state of Connecticut, with a maximum diameter of 93 miles (fig. 2). Its area is greater

[1] MACCAUGHEY, V., The little end of Hawaii. Jour. Geography 15:23–26. 1916.

than that of all the other islands combined. It is composed of 5 volcanic masses. The northernmost, the Kohala Mountains, is of extreme antiquity, deeply eroded, and probably as old as Kauai.

FIG. 1.—Island of Hawaii, showing high mountains and principal recent lava flows.

Mauna Kea and Hualalai, next toward the south, have become "extinct" within comparatively recent times; a lava flow issued from Hualalai in 1801. Mauna Kea has given no manifestations of activity within historic times. It is the highest point within the North Pacific Ocean.

The two southern mountains, Mauna Loa (figs. 6, 7) and Kilauea, are active volcanoes. Their summit craters have exhibited spectacular activity at intermittent periods throughout historic time, and vast lava flows have emanated from their flanks. A large flow issued from the southern slopes of Mauna Loa in May 1916. Loa dominates the island of Hawaii and is the greatest volcanic mountain in the world. The elevations of 5 volcanic

FIG. 2.—Island of Maui: Mount Haleakala comprises entire eastern lobe of island; lava flow country at summit, in caldera, and on southeastern slopes of mountain; regions are largely xerophytic, with exposed lava fields, fields of cinder and ash, cinder cones, and pit craters.

masses of Hawaii are as follows: Kohala Mountains, 5489 ft.; Mauna Kea, 13,825 ft.; Hualalai, 8269 ft.; Mauna Loa, 13,675 ft.; Kilauea, 4000 ft.

HALEAKALA ON MAUI.—Haleakala (fig. 8) is the great mountain that forms the entire eastern portion of the island of Maui. The summit is 10,032 ft. above sea level. It contains a great volcanic caldera, one of the largest in the world, 7.5 miles long by 2.5 miles wide and over 2000 ft. deep. This mountain, often called East Maui, is very much younger than the deeply eroded western mass.

FIG. 3.—Tufa cones and xerophytic lava fields, Oahu; open crater to right, Koko Crater; hill beyond to left, Koko Head.

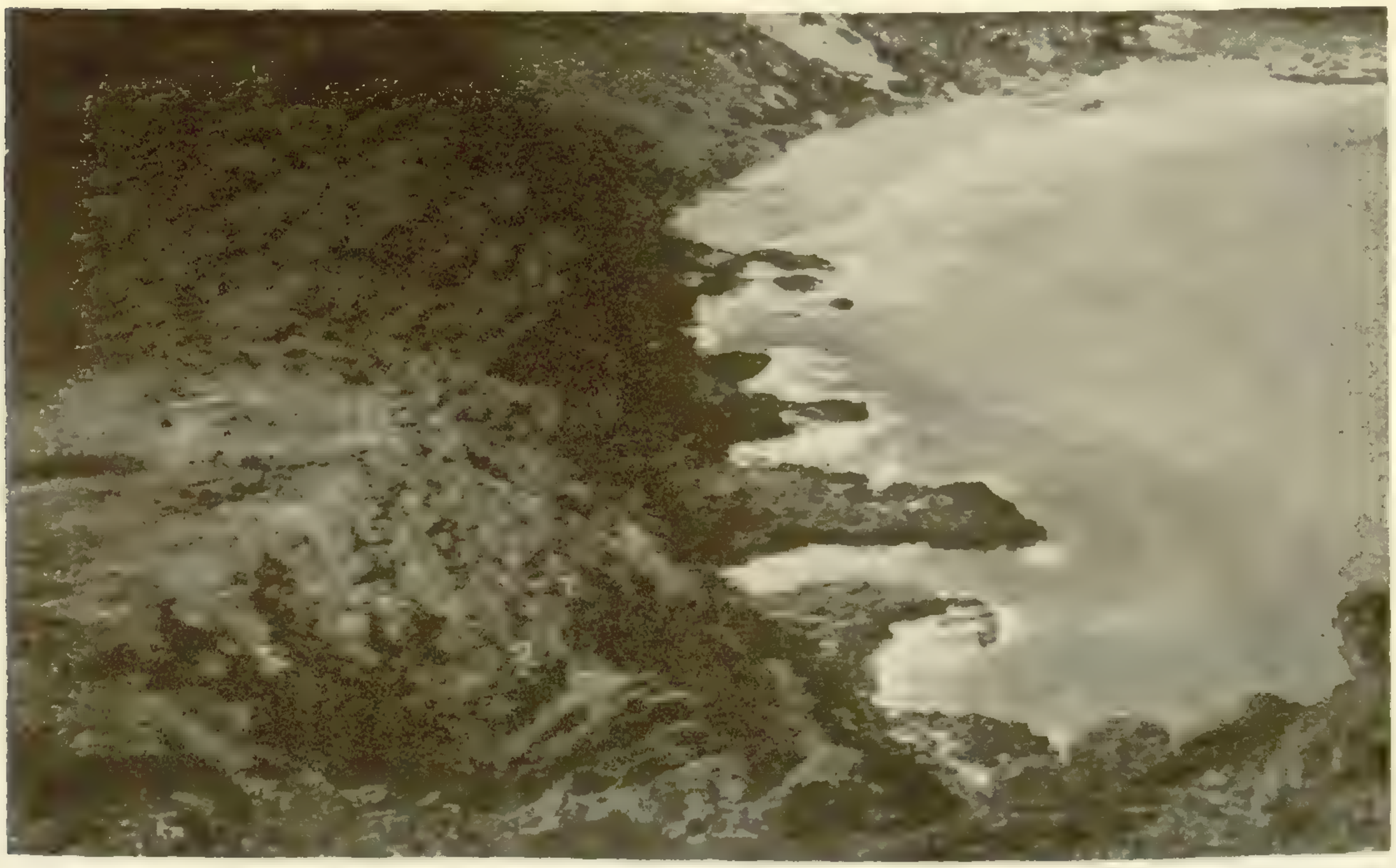

FIG. 4.—Arid headland, Maka-pu'u, Oahu, illustrating ancient lava sheets exposed by extensive erosion; note stratification of lava flows and erosion of flows at sea level.

Maui is a volcanic doublet made up of two masses of widely different ages. Haleakala probably ceased activity at about the same time as Mauna Kea. The windward, northern face of Haleakala, like that of all the Hawaiian mountains, receives torrential rainfall (400 inches per annum) and is densely covered with jungle forest. The leeward, southeastern slopes are conspicuously arid and barren. In its geological and botanical aspects Haleakala is much more closely related to Kea and Loa on Hawaii

FIG. 5.—Manana or Rabbit Island, deeply eroded tufa cone, isolated as small *barren* islet off windward coast of Oahu, near Maka-pu'u Point; about 2200 ft. long and 400 ft. high, separated from main island by channel of 1 mile; vegetation sparse and stunted, no arborescent vegetation.

than to its associate West Maui. It is separated from Hawaii by a relatively narrow channel, 26 miles wide and 1032 fathoms deep. From the standpoint of this paper it will be considered as one of the Kea, Loa, Hualalai family.

THE FOUR GREAT MOUNTAIN MASSES.—These four great volcanic mountains, Haleakala, Kea, Loa, and Hualalai, closely resemble each other in a number of important ecological particulars: (1) their summits rise 8000–14,000 ft. above sea level and are frequently covered with snow; (2) there is a large treeless zone on the summit of each; this is most extensive on Loa, Kea stands next, then

FIG. 6.—Summit and upper slopes of Mauna Loa as seen from summit of Mauna Kea; note very gentle slopes of Loa, and two cinder cones (explosive vents) in foreground.

FIG. 7.—View of Loa from summit of Hualalai; clouds lying at elevation of 7000–8000 ft.; note xerophytic vegetation in foreground.

Haleakala, and lastly Hualalai, the smallest of the four mountains; (3) the summits are marked by volcanic vents; either an active crater (Loa); or an extinct caldera (Haleakala); or great numbers of cinder cones (Kea); or by innumerable pit craters and cinder cones (Hualalai); all of these are large and tangible evidences of the earth forces by means of which the mountains were built up to their present height; (4) the mountains rise directly and gradually from the sea, without intervening lowlands or plateaus; (5) the

FIG. 8.—Cinder cones on floor of Haleakala caldera; at extreme upper left are some silver sword plants (*Argyroxiphium sandwicensis* var. *macrocephalum*).

slopes and flanks of each mountain are covered by thick blankets of lava, cinders, and ash, which in the arid summit and leeward regions have undergone little or no erosion; (6) each mountain has a lower windward region which receives heavy precipitation; this rain, amounting to several hundred inches per annum in many localities, has caused the rapid decay of the lava flows in these zones and has covered the flows with luxuriant rain forest; the original flow structure is obliterated beneath heavy beds of soil and vegetation. This paper does not include the humid areas.

Cinder cones

The slopes and summits of all four of the great mountains are thickly sprinkled with cinder cones (fig. 9). These vary in height from 200 to 1000 ft., with very steep slopes of 30–40°. They are composed of volcanic ash, cinders, scoria, and other ejecta, and are frequently strewn with volcanic bombs and other lava blocks. These cones are most numerous on Kea and Hualalai; they are plentiful in the caldera of Haleakala and on the leeward slopes, and are by no means infrequent on the broad flanks of Loa. Many of these cones are more or less completely covered with vegetation and are conspicuous from a distance, serving as landmarks.

FIG. 9.—Summit plateau of Mauna Kea, showing numerous cinder cones; these explosion cones are abundant on all high mountains of Hawaii, from sea level to summit regions.

PIT CRATERS.—A second type of volcanic vent of distinct ecological interest is the pit crater (figs. 10, 11). This is typically a circular pit, its mouth flush with the surrounding country, its walls vertical or funnel-shaped, and its floor littered with volcanic débris. In diameter these pits vary from a few feet (200–300 ft. in the case of the smaller ones) to several miles in the case of the gigantic pits of Kilauea and Loa. The pits of greatest botanical interest are those of intermediate size, namely, 100–300 yards in diameter and of similar depths. There are many pits so deep and narrow that no floor is visible from the rim.

The pit craters occur indiscriminately in the rainy forest zones and on the barren slopes and summits. In the former case they are densely filled with trees and jungle litter; their mouths are often hidden by vines and other vegetation, and they constitute a serious menace to the traveler and to livestock. Those that occur in the arid sections are of particular botanical significance, as their steep walls prohibit invasion by cattle and goats, and the vegetation within them is unmolested. Thus they constitute botanical

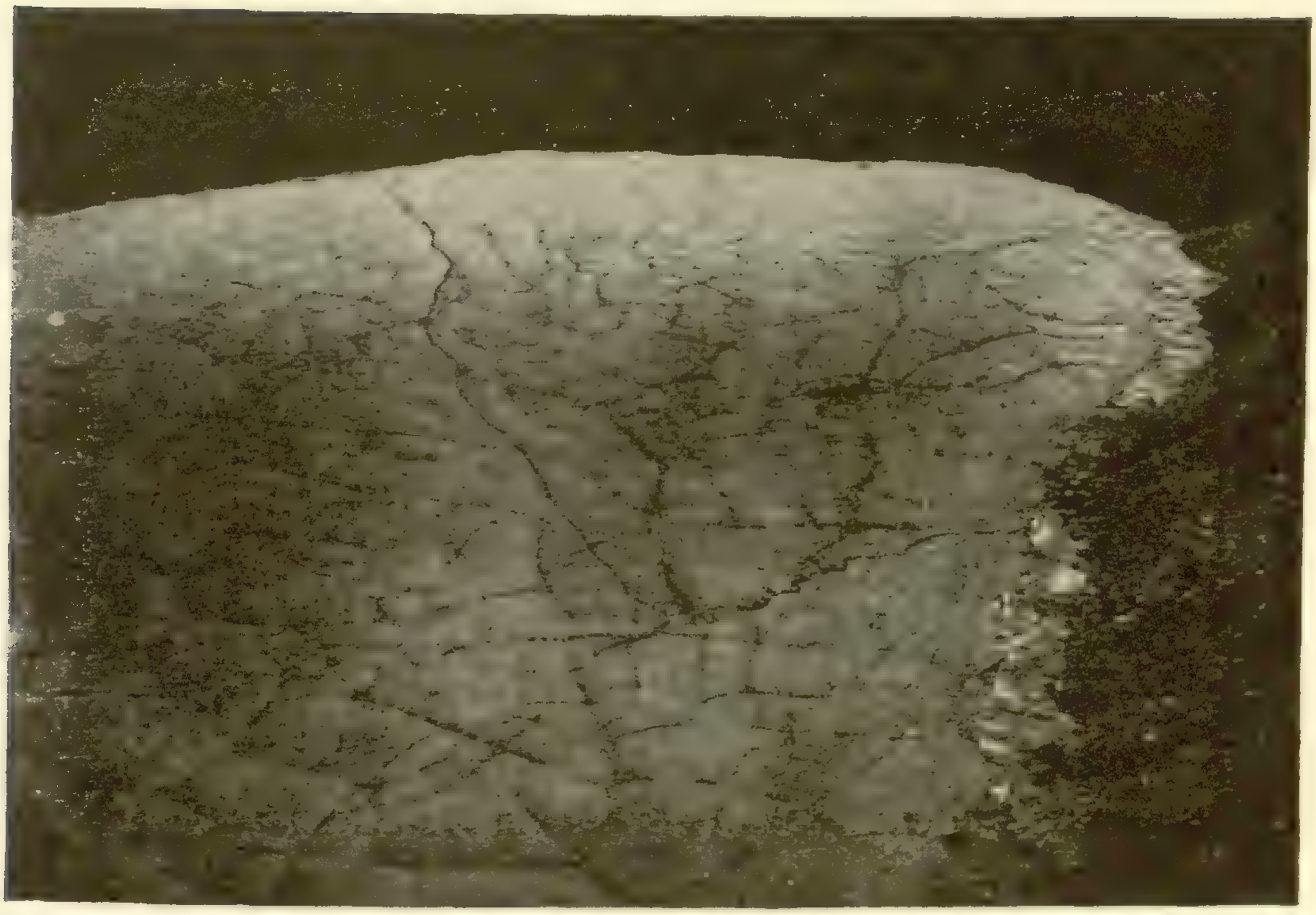

FIG. 10.—Floor of pit crater, close to Kilauea, fissured in mosaic manner with remarkable regularity; although nearly 40 years have passed since last eruption, there has been practically no plant invasion in this crater, due to its unfavorable situation.

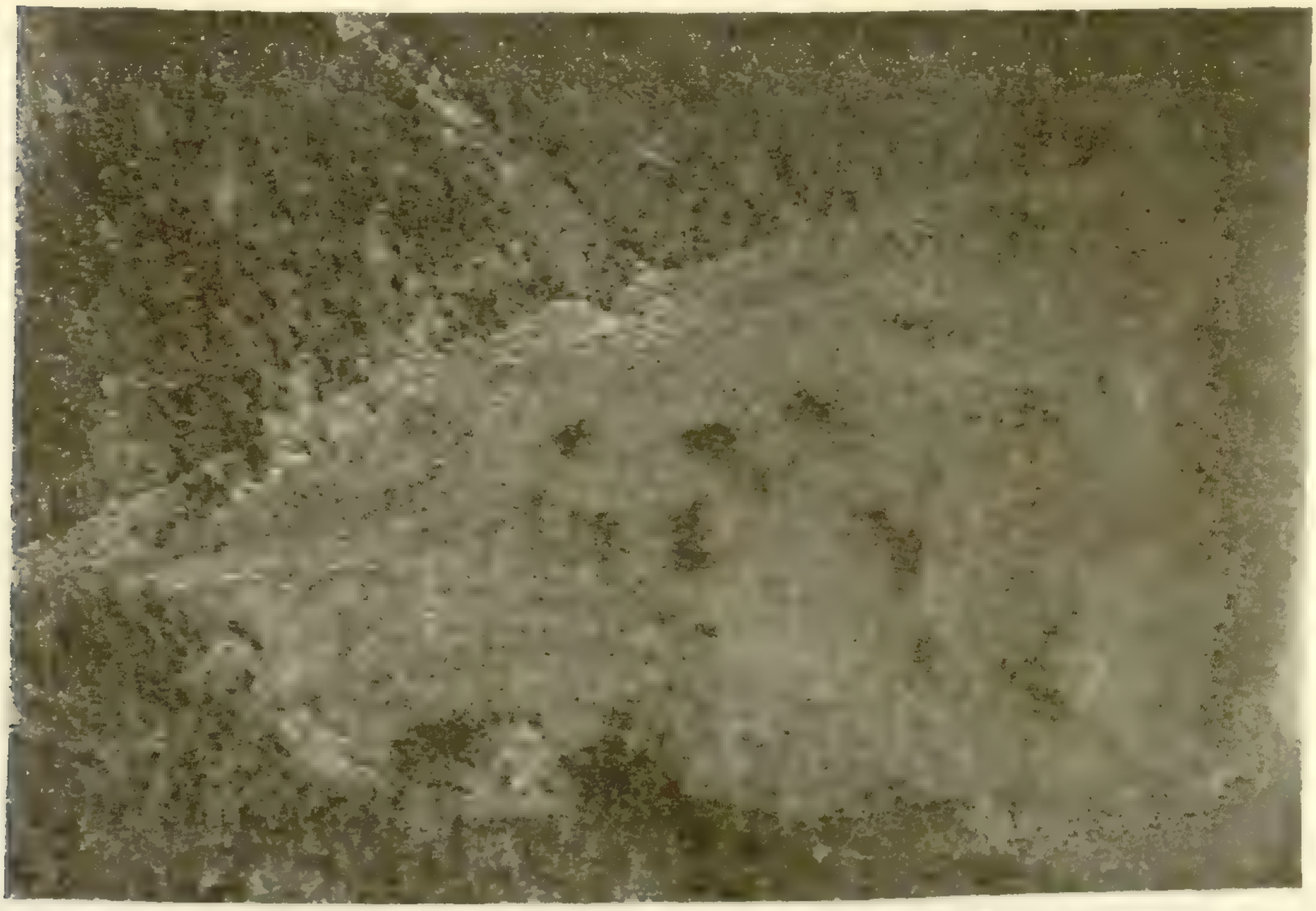

FIG. 11.—Floor and wall of pit crater close to Kilauea, largely covered with *pa-hoe-hoe;* walls covered with *Metrosideros polymorpha*, 10–20 ft. high.

oases in otherwise barren country and may be compared with the *kipukas* in the *a–a* flows. Many remnants of the primitive flora are today making their "last stand" in these tiny areas where they are protected from wild livestock, the greatest enemy of the indigenous vegetation. Finally, the conditions of shade and moisture

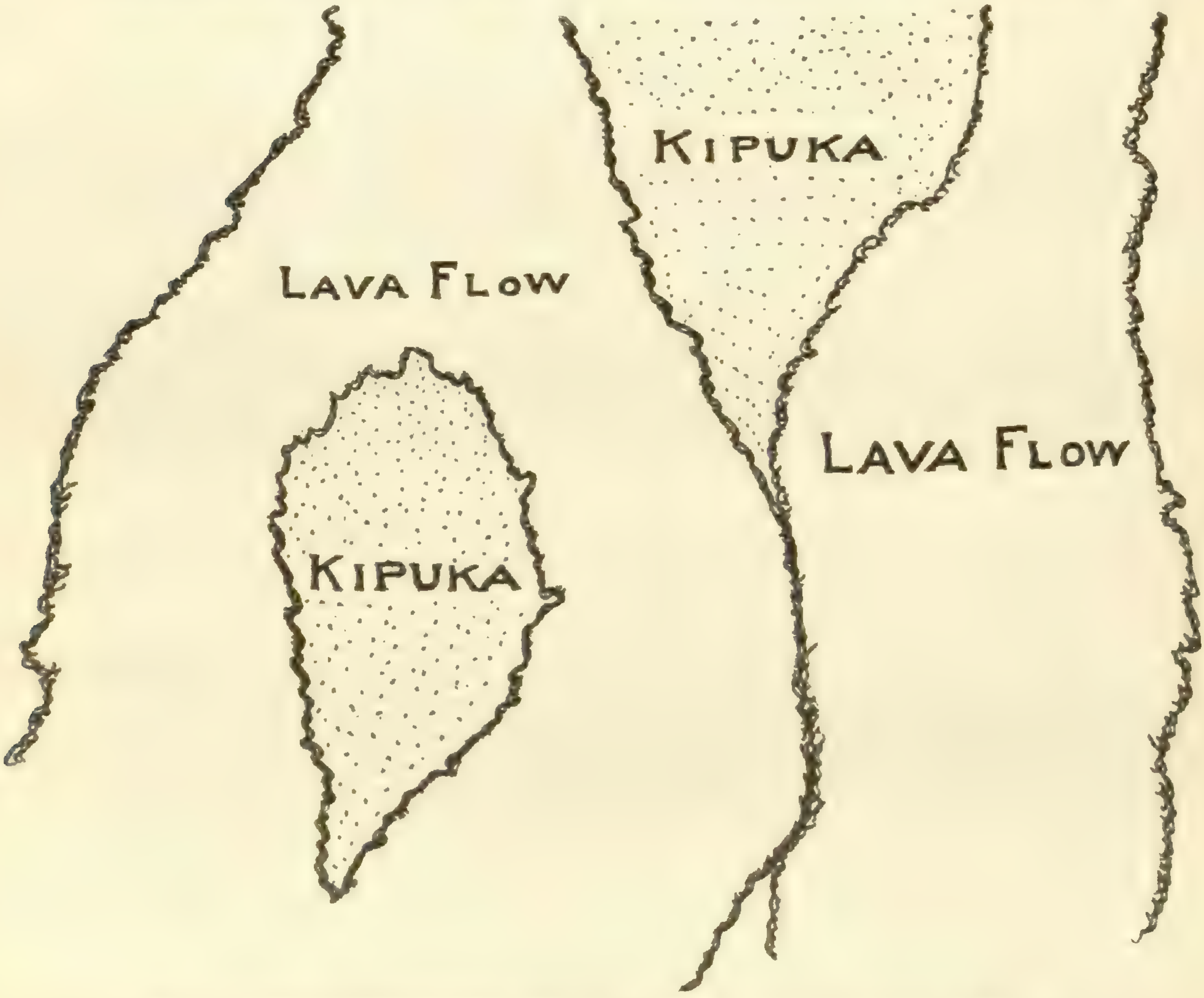

FIG. 12.—Diagram illustrating formation of kipuka in midst of lava fields.

are more likely to be favorable in the pits than on the exposed open lava flows, and the plants in the pits exhibit more normal growth forms than those in the open.

KIPUKAS.—This Hawaiian word, meaning an oval hole or depression, is a convenient designation for small areas that, owing to minor topographical irregularities, have escaped being covered by the lava flows which surround them (fig. 12). The flow may be

split or deflected so that these small patches of forest remain unscathed. Like the pit crater, the kipuka is often a botanical garden in the midst of an arid waste land.

The lava which surrounds the kipuka, and which may be 15–30 ft. higher than the floor of the latter, serves as a protection from wild cattle and goats. The kipukas frequently contain a very rich flora, a remnant of the original forest cover. These patches are usually of very limited area, not more than 2 or 3 acres, and are sharply limited by the impinging lava beds. The soil within the area is usually deep, black, and rich, and of great antiquity. There are hundreds of these kipukas on the lower slopes of the great Hawaiian volcanoes, but only those in the arid regions retain their individuality. Those in the humid regions are hidden under the rain forest.

PUU WAA-WAA.—An ancient cone of minor topographical importance, but of extreme interest from the standpoint of the geological and botanical history of the archipelago, is Puu Waa-waa, in North Kona, Hawaii. This cone is about 6 miles north of the summit of Hualalai, near the Loa flow of 1859. Its elevation is about 3300 ft. above sea level. It is 500 ft. high, with steep, deeply fluted sides. The numerous erosion ravines which radiate from the summit and produce this corrugated appearance (the native name means "fluted hill") are 50–75 ft. deep. The cone is composed of volcanic ash and cinders, and exhibits the quaqua-versal structure of the typical explosive cone. It has been deeply encircled by lava streams from Hualalai and Loa.

Studies by CROSS[2] of the lavas which underlie Puu Waa-waa have demonstrated that these lavas are trachytic, and vastly older than the basaltic lavas which now largely cover them. This hill is undoubtedly a vestige of an ancient island mass now submerged beneath newer lava. Botanical explorations by ROCK have strikingly confirmed the antiquity of the Puu Waa-waa region as contrasted with the much younger regions which surround it. Many evidences of a primitive flora have been found, a flora that has largely disappeared from other portions of this

[2] CROSS, WHITMAN, An occurrence of trachyte on the island of Hawaii. Jour. Geol. 12:510–523. 1904.

island. The Puu Waa-waa region, like some of the pit craters and kipukas, is a botanical oasis in the midst of a desert and harbors much material of unquestionable antiquity.

VOLCANIC DUST.—In order to treat comprehensively the ecological aspects of the lava regions, it is necessary to include a statement concerning volcanic dust (fig. 13). The Hawaiian volcanoes have

FIG. 13.—Pumice fields, Kilauea volcano; chief plants, *Metrosideros polymorpha* and various xerophytic species; white patches in foreground, lichens; in distance, to right, is ohia forest, *Metrosideros polymorpha*.

been conspicuously quiescent in their activities during historic times; the outpourings of lava have been relatively gentle and non-explosive. There is much evidence, however, which indicates tremendous explosive eruptions at various periods in the history of the volcanoes, and at least one of these (Kilauea, 1790) has fallen within historic times.

Among the most abundant of the varied products of these explosive eruptions, in the Hawaiian Islands as in the case of volcanoes generally, is volcanic dust. Extensive deposits of dust

occur on the leeward slopes of Haleakala and in the caldera itself; on the leeward slopes of Kea and Loa; and great beds to the leeward of Kilauea. Perhaps the largest area is in the Ka-u district, where, according to HITCHCOCK,[3] it covers "an area of 300 sq. mi." It is not within the province of this paper to enter into any detailed account of these dust deposits, but two important floristic relations may be enumerated: (1) the obliteration of any vegetation that may have occupied the region previous to the deposit; (2) the thick layer of ashes, if rainfall or irrigation be sufficient, forms a rich and mellow soil and transforms what would otherwise have been lava waste land into productive country. The plantations and ranch lands of Ka-u owe their origin to this. It may be pointed out, in conclusion, that similar deposits of volcanic ash, of great area and thickness, occur in Central America, Mexico, the Sierra Nevadas, the Great Basin, Utah, Montana, South Dakota, Nebraska, Kansas, Washington, Oregon, Alaska, Canada, and many other places.

Ecological factors

SLOPE.—There is considerable variation in the gradient of the various high mountains, but on the whole it is remarkably gentle. Loa has a deceptively gentle slope, averaging 4–6° and not over 8° at the steeper places. Its outline against the sky is that of a very much flattened dome, or "whaleback." The slopes of Kea and Haleakala are more abrupt, usually about 12°, but sometimes as high as 15°. Hualalai is the steepest of the 4 mountains, particularly near its summit, with an average slope of 14–18°. The cinder and ash cones have slopes which lie at the critical angle for material of this character, namely, 30 or 40°. The mountains are all relatively young and have not been carved by deep, precipitous-walled amphitheaters of erosion, as have the mountains of Kauai, Oahu, eastern Molokai, and West Maui.

PRECIPITATION.—The only comprehensive records of rainfall in the Hawaiian Islands are those made by the United States Weather Bureau and the United States Hydrographic Survey. The records of the former are collaborated from the reports of

[3] HITCHCOCK, C. H., Volcanoes of the Hawaiian Islands, p. 153.

about 50 observers, scattered at various points on the islands. As these observers are stationed in or near human settlements, and as these settlements are situated in regions of at least moderate rainfall, it happens that there are no records covering the areas which form the central theme of this paper. The great upper slopes of Loa, Kea, Hualalai, and Haleakala, having a total area much greater than that of the peripheral lowlands, are uninhabited waste lands and without meteorological data comparable to that of the agricultural lowlands.

The Hydrographic Survey, interested primarily in the rain sections and the streams, has naturally avoided the great arid and streamless areas which are considered in this paper. Hence it is not possible to present extensive tables showing accurately the precipitations on these arid districts.

It is necessary to emphasize the importance of the trade winds as the rain-bearing winds of the islands. These winds blow from the northeast almost continuously through a large portion of the year. The main axis of the archipelago lies from northwest to southeast, so that the islands lie across the path of the trades, and hence develop strongly differentiated windward and leeward climates. The warm trades sweep across vast stretches of ocean before reaching the islands, and are consequently saturated with moisture. Upon striking the cool mountain slopes very heavy precipitation ensues, often totaling several hundred inches.[4] In this zone the luxuriant rain forest reaches its finest development. The leeward slopes, however, are robbed of this torrential rain; the winds that reach them are usually dry and parched, and the climate is arid or semiarid.

SNOW AND ICE.—The high mountains of Maui and Hawaii are often snow-capped. This is particularly true of Kea, literally the "white mountain," which is prevailingly snow-crowned from November to March and intermittently at other seasons. At the season of greatest snowfall the snow line often reaches down as low as 9000 ft.; at other seasons there are frequently extensive patches of snow at the higher levels. Near the extreme summit

[4] The greatest annual precipitation officially recorded in the Hawaiian Islands is 561 inches, in 1916, on Waialeale, Kauai, by the Hydrographic Survey.

of Kea, at an elevation of 14,000 ft., is a small perennial pond, Wai-a'u, about 125 ft. in diameter. This pond is situated in an ancient crater basin and is fed by the melting snow. It is frozen during a major part of the year, even in midsummer. Ice occurs in the deep fissures and caverns in the neighborhood of the summits of Kea and Loa throughout the entire year, and during late winter it is relatively abundant.

SUMMIT REGIONS.—The treeless character of the summits has already been mentioned. The timber line is very low, indeed unusually low as compared with that of mountains in other parts of the world. HALL'S[5] explanation so accurately summarizes the local conditions that it is reproduced herewith:

> Elevation has put a sharp limit to the forests on the islands of Hawaii and Maui at from 6000 to 8000 ft. This leaves very large areas of Mauna Loa, Mauna Kea, Hualalai, and Haleakala devoid of forest, and they have always been so. The mountains of the other islands, being under 6000 ft., are forested to their summits. Six to 8000 ft. is a surprisingly low timber line, considering the favorable conditions of soil, moisture, and temperature which prevail at that altitude in Hawaii. The sufficient reason seems to be that the species composing the native forests are all representatives of the torrid zone, and in these islands, which lie right at the edge of the Tropics, find their limit at the low altitude named.

SEEPAGE.—The physical structure of the lava flow is such that seepage takes place with extreme rapidity, and in the typical flow country there is absolutely no surface water. This abnormally high percolation greatly heightens the physiological aridity of the lava as a substratum for plant life. Both the *a-a* and the *pa-hoe-hoe* types of lava are highly ramified with crevices, caverns of all sizes, and long tunnels or lava "tubes." Thus a vertical section of the mountain would reveal a copiously spongy texture, with large caverns sloping toward the sea. DANA'S[6] account may be appropriately quoted in this connection:

> Over the leeward sides . . . . where rains are infrequent, a black desert everywhere prevails, and there is, with rare exceptions, only an alternation between the smoother fields of cooled lava and the rougher districts of scoria. Yet over the barest fields there is always a sprinkling of verdure, growing

[5] HALL, W. L., Forests of the Hawaiian Islands. 1904 (p. 16).

[6] DANA, J. D., Geol. U.S. Explor. Exped. **10**:1849 (pp. 159–160).

from the many crevices or cavities. Whatever showers fall on this portion of Hawaii are at once absorbed by the cavernous rocks; and consequently through its whole extent, south and east, there are not two permanent streamlets. Water is to be found only in caverns; and often a journey of some miles must be taken by the villager to supply himself for his daily consumption. All the caverns about the lower parts of the mountains have been well explored for this necessary of life.

There is probably no other region in the world where rainwater disappears with greater rapidity than on the leeward slopes of the Hawaiian Mountains. The honeycombed lava flows swallow it up, and convey it to the sea through deep subterranean channels. Thus the aridity of the lava country is compounded by 3 factors: low precipitation, high evaporation, rapid percolation.

EVAPORATION.—An ecological factor of probably greater importance than either precipitation or percolation is that of high evaporation, which characterizes the Hawaiian flows, as it does all arid regions. This very high evaporation is strongly productive of xerophilous structures and is probably more potent than any other single factor.

The lava flow

In order to elucidate the structural peculiarities of the lava country as related to plant life, a brief synopsis of the formation of a typical flow may be presented. This is adapted from HOBBS'S[7] account.

The lava either quietly melts its way to the surface at the time of outflow, or else produces one or more fissures for its egress to the accompaniment of vigorous local earthquakes. In either case, if the lava issues at a point far below the crater, the hydrostatic pressure causes gigantic lava fountains to arise at the point of outflow. The fluid, incandescent rock shoots up to heights which range from 200 to 700 ft. or more above the surface. In the 1852 eruption of Loa a fountain of lava 1000 ft. broad rose to a height of 700 ft. A certain proportion of this fluid lava is sufficiently cooled to consolidate while traveling in the air, and upon falling it builds up a cinder cone. This cone becomes a location

[7] HOBBS, W. H., Earth features and their meaning. Macmillan. 1912 (pp. 110–111).

monument at the place of discharge. Cones of this sort are plentiful on the slopes of Loa and Kilauea. From this outlet the lava begins its journey down the slopes of the mountain. The surface quickly freezes over and produces a tunnel, beneath the roof of which the fluid lava flows with comparatively slow further loss of heat. It empties its own tunnels, and in this way the long lava tubes, beneath the flows, are formed. The great lava streams that flow down the side of Loa sometimes attain a length of nearly 50 miles, and occasionally enter the sea. They are often 2 or 3 miles broad. DANA estimated the 1852 flow to contain over 10,500,000 cu. ft. of lava. The low angle of slope presented by the flanks of the mountain, and its nearly flat summit, are due to the tendency of the sheet of liquid rock to travel far and spread widely before cooling. It is by the successive additions of such sheets that the mountain has been built up.

It is of interest to note RUSSELL'S[8] statement concerning the great Columbian lavas of the Northwest, which cover an area of 200,000–250,000 sq. miles. He points out that this is "not one vast flow, but is composed of many independent sheets, which are sometimes separated by land surfaces containing the stumps of trees and even huge trunks buried in lapilli and now thoroughly silicified."

SURFACE OF LAVA FLOWS.—There are two principal types of lava forming the Hawaiian flows, which determine the general surface and structure of the flow: *Pa-hoe-hoe*, the native word for smooth or shining, designates the smooth pavement type (figs. 14–17). The crust is glassy and frequently quite brittle. Hummocks or mounds are frequent, due to the rapid cooling of the surface. Some of these mounds are quite small, others may be 30–40 ft. high and twice as long, the thick crustal layers being broken and heaped like "pack" ice. The surface of the *pa-hoe-hoe* is commonly of a ropy or festooned pattern. The wrinkles and furrows have their convex arcs downstream, as the velocity is greater in the center than at the sides. As the smoother, pavement-like parts of the flow cool, vertical cracks develop in every direction, forming a coarse network or mosaic pattern. The distance

[8] RUSSELL, I. C., Volcanoes of North America. Macmillan. 1897 (p. 250).

between these cracks is commonly every 2 or 3 ft. in all directions. The flow is thus broken up into irregular polyhedral blocks, which tend to separate under weathering and gravity. In old flows these cracks may become several inches wide and are commonly utilized by plants as growing places. The fresh *pa-hoe-hoe* is shining jet

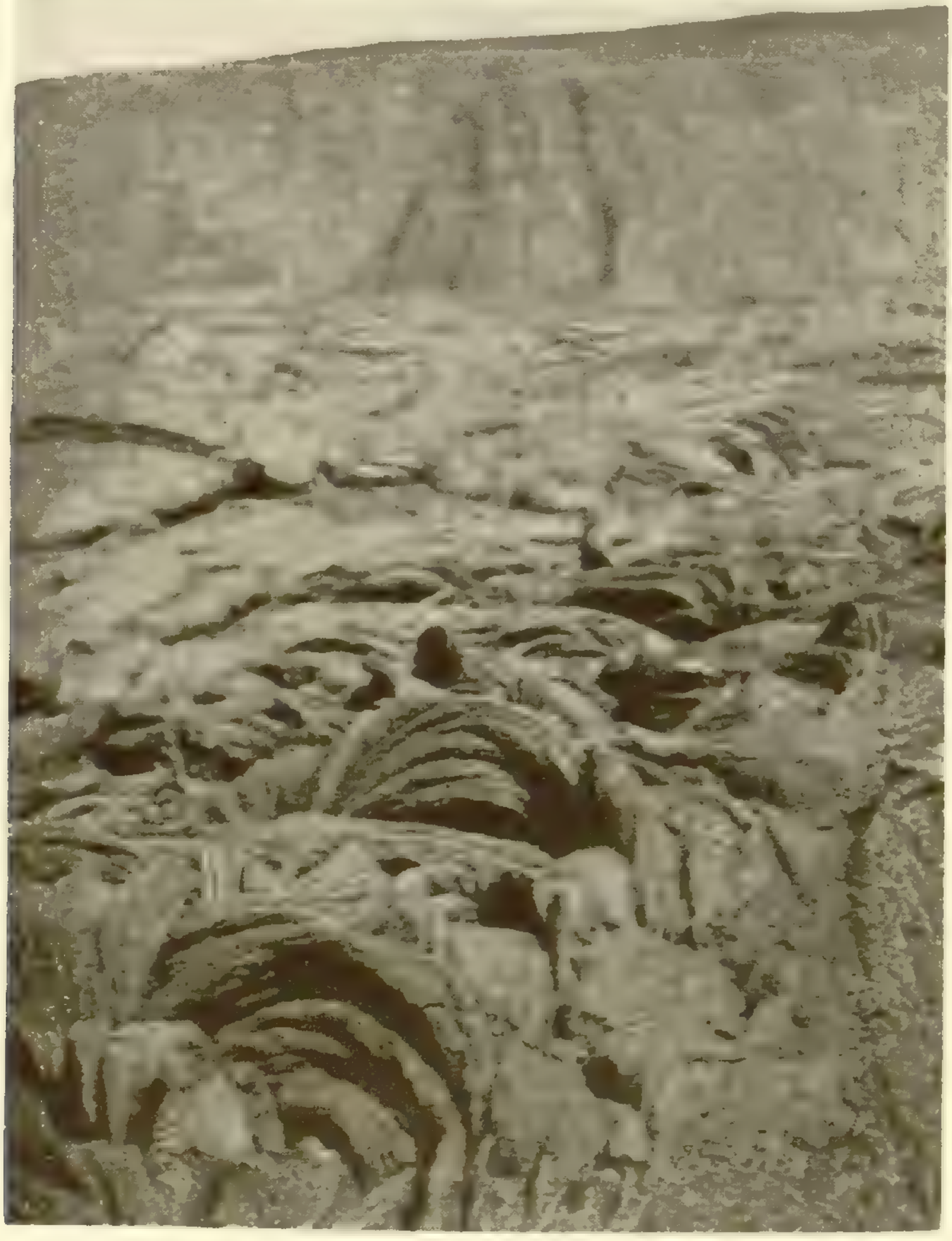

FIG. 14.—Close view of ropy or festooned *pa-hoe-hoe* on floor of Kilauea; note concave upper faces of festoons in which seeds and spores are caught and plant life first established.

black and in arid situations retains this appearance for an indefinite period. Under humid conditions, however, it weathers rapidly and becomes brown or reddish, due to the oxidation of its high iron content. On the *pa-hoe-hoe* fields the plant life occurs chiefly in the furrows or wrinkles of the ropy areas and in the numerous fissures that are abundant in the surface of the smoother areas.

FIG. 15.—Mound of *pa-hoe-hoe* lava, on floor of Kilauea crater, composed of heavy slabs of vesicular lava; surface conspicuously festooned or ropy.

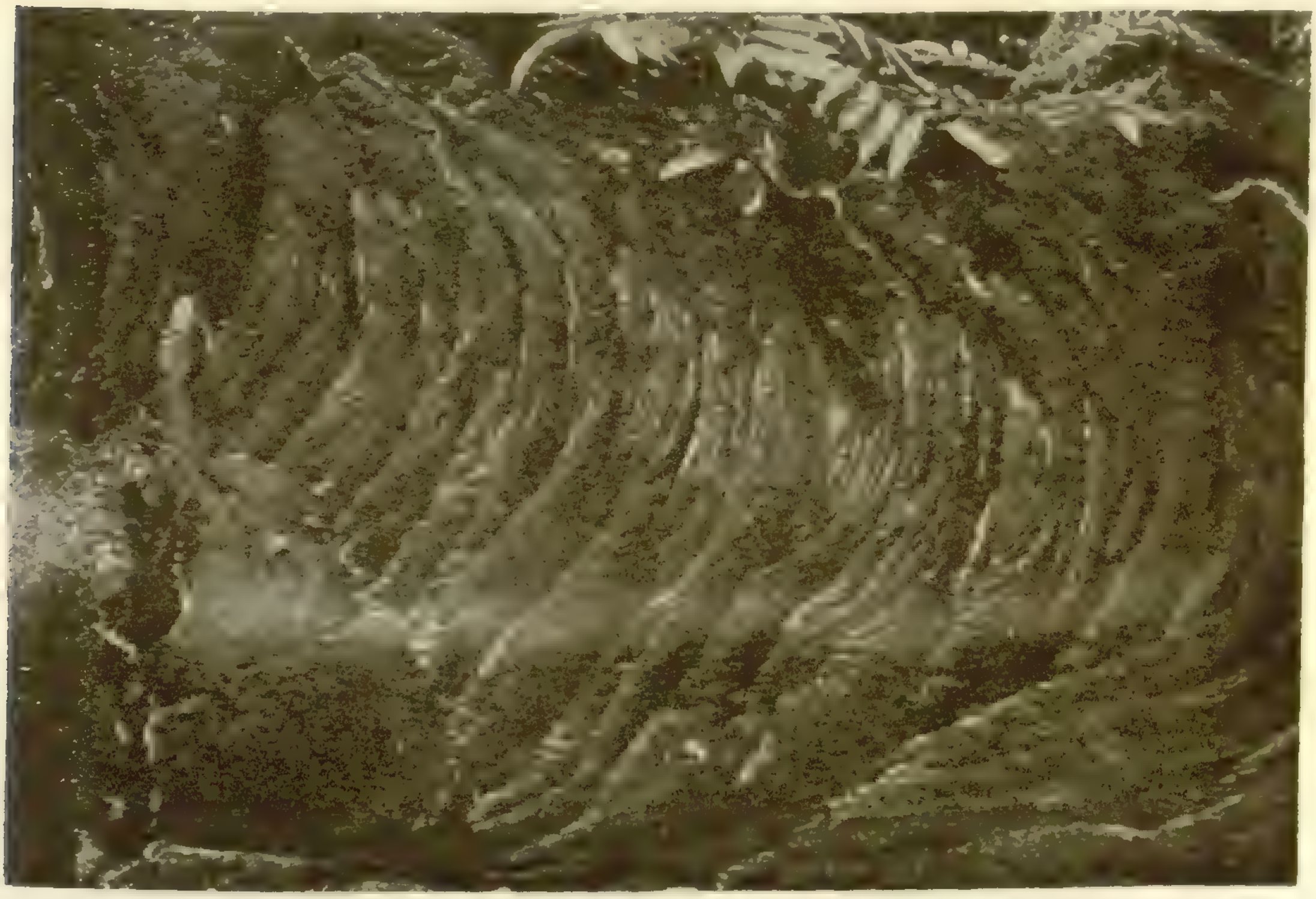

FIG. 16.—Surface of festooned *pa-hoe-hoe;* note abundant lichen growth both in crevices and on protuberances; fern is *Polypodium pellucidum.*

A-a is exceedingly rough lava (fig. 18) composed of incoherent, bristling spiny blocks of all sizes, like gigantic clinkers. DANA says (*loc. cit.*, p. 162):

> They look as if the mountain had been shattered to a chaos of ruins. The fragments vary from 1 to 10,000 cu. ft. or from a half bushel measure to a house of moderate size. They are of all shapes, often in angular blocks, sometimes in slabs, and have a horrible roughness beyond conception, points and angles standing out in every direction; they lie together, touching only by their edges or points, leaving deep recesses everywhere between them.

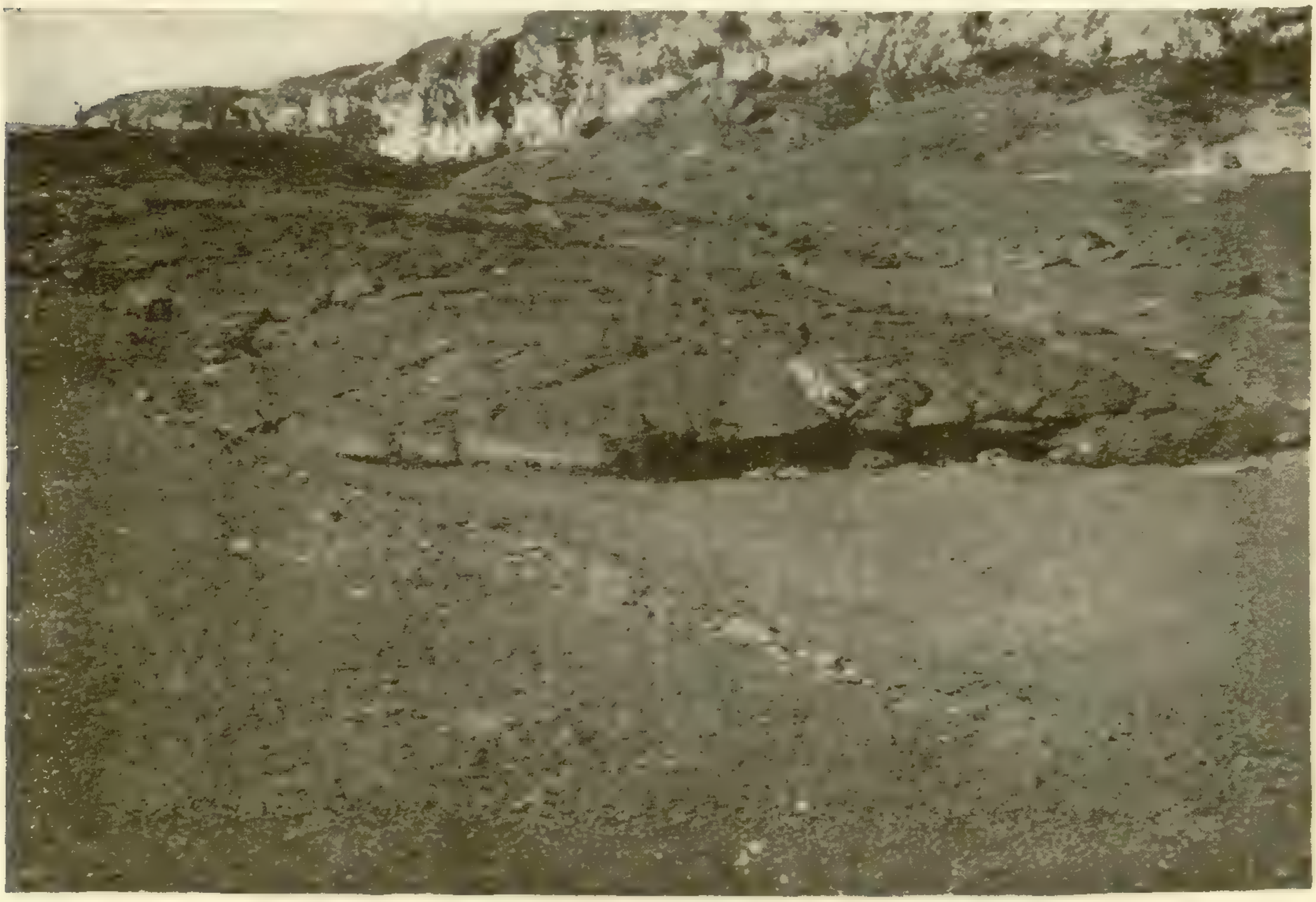

FIG. 17.—Front or end of *pa-hoe-hoe* flow in crater of Kilauea; note smooth character of surface and lobular margin; plants here and there along margin are *Vaccinium reticulatum*.

The beds are 30–60 ft. thick, with innumerable cavities between the blocks. On very old *a-a* flows the blocks and finer material have settled somewhat, rendering the entire mass more compact; the surface material is also less spiny. *A-a* flows are so rough as to be practically impassable by man or beast, and in traveling across the lava wastes one is compelled to make long detours to avoid them. The sharp cutting edges quickly destroy even the

heaviest leather boots. Horses, cattle, and goats use the *pa-hoe-hoe* as natural roadways but refuse to cross the *a-a*. It is due to this impassability of the *a-a* that plants growing upon it, or in areas surrounded by it, are protected from the devastations of herbivorous animals. Thus portions of the primitive flora have been preserved in regions where they would have otherwise been de-

FIG. 18.—Front or end of 1917 flow, which issued from flanks of Loa, composed of *a–a*, flowing over older *pa-hoe-hoe;* smoke arising from various portions of flow; note angular fragments of which *a–a* is composed, tree at lower left is *Metrosideros polymorpha.*

stroyed by wild cattle and goats. *A-a* lacks the glistening appearance of *pa-hoe-hoe* and is usually dark chocolate brown instead of black. Sometimes the reddish tint is quite pronounced. The brown and red are due to the high iron content, which characterizes all the Hawaiian lavas.

CHEMICAL COMPOSITION OF LAVA.—The following table illustrates the chemical composition of a typical Hawaiian basaltic

lava and is selected from a large series collected by H. S. WASHINGTON (U.S. Geol. Survey, Professional Paper no. 14). The

SiO_2	49.01	K_2O	0.80
Al_2O_3	16.29	TiO_2	3.93
Fe_2O_3	7.61	P_2O_5	0.49
FeO	4.89	MnO	0.27
MgO	3.62	SO_3	0.20
CaO	9.79	S	0.02
Na_2O	3.82	CuO	0.10

soils derived from the weathering of these basaltic lavas are very different from those common on the mainland of the United States. Burgess[9] states as follows:

> They are primarily basic in composition, whereas those of North America, for example, are acidic.. The bases or framework of Hawaiian soils are the oxides of iron and aluminum, whereas the basis of mainland soils is silica. A glance at the following table will show these great differences better than words can express them. These figures represent averages of large numbers of soil analyses made by the "absolute" or "fusion" method. The column marked "Mainland soils" represents averages of soil analyses from almost every state in the Union and from provinces in Canada. The column labelled "Hawaiian soils" gives average figures for over 300 composite samples of soil from the leading types on all of these islands. All of these analyses were made here and under similar conditions.

	Hawaiian soils	Mainland soils
	Per cent	Per cent
Basic constituents	63.717	18.980
Acidic constituents	36.458	81.014
$Fe_2O_3+Al_2O_3$	59.240	13.250
CaO	0.698	0.830
MgO	1.242	0.771
K_2O	0.737	1.622
Na_2O	1.420	2.229

The prevailing low summit temperatures have already been noted. The annual mean temperature of Mauna Loa at the timber line is estimated by the United States Weather Bureau as 50° F. and the summit temperature as 35°. The Bureau states "in the

[9] Rept. Haw. Sugar Planters' Expt. Station, Honolulu. 1915 (p. 62).

absence of actual observations in the higher levels, a temperature decrease of 1° F. is assumed in each 320 ft. of ascent."[10] The annual mean summit temperature of Kea is given as below 30°. It should be emphasized that very much lower temperatures than these prevail during a considerable portion of the year, especially at night, and are accentuated by the high winds. During the brilliant cloudless day the black lava sheets absorb great quantities of heat, and the aerial temperatures near the ground become very high. At nightfall, however, a very rapid chilling of the air ensues, and the thermometer drops in a few hours to the neighborhood of freezing point. This sudden drop is familiar to all who have ascended the high peaks. This wide diurnal range of aerial summit temperatures is in striking contrast to the equable and monotonously invariable temperatures of the littoral regions.

TEMPERATURES OF LAVA AND CINDER FIELDS.—Reference has already been made to the low temperatures which prevail at the summit regions. Another phase of this extremely interesting ecological factor remains to be considered, namely, the comparatively high temperatures which characterize the lava and cinder fields themselves during the daytime. All of these volcanic deposits are black or very dark in color. They absorb vast quantities of heat during the uninterrupted diurnal period of insolation. Those who have traveled across the lava waste lands well know that by the middle of the afternoon the surface of the rock is distressingly hot. The surface, the rock layer immediately below it, and the aerial layer immediately above it have temperatures much higher than the prevailing aerial temperatures. This condition is similar to that reported by investigators of other desert regions. MACDOUGAL[11] notes that "the sandy soil around the roots of small herbaceous plants in the Grand Canyon, Arizona, ... exhibited temperatures as high as 148° F." It is to be further noted, as MACDOUGAL states (*loc. cit.*, p. 77), that "these extreme temperatures are met only by the roots of species spreading in the surface layers of the soil." Deep-rooted species are not so likely to be affected.

[10] U.S. Weather Bureau, Hawaii Station, Ann. Rept. 1915 (p. 2).

[11] MACDOUGAL, D. T., Botanical features of American deserts, p. 82.

No thermograph records are available for subterranean temperatures in the Hawaiian lava flows, but such will very likely correspond closely with the results obtained by Cannon.[12] In his study of the root relations of desert plants at Tucson, an almost continuous record was made of the soil temperatures at a depth of 15 cm. for the 5 years 1905–1909. CANNON states:

> The record shows an undulating record of which the curve crests correspond to the warmest for each day, and the depressions the coldest. The crests . . . . are remarkably uniform in height, as also the depressions are uniform in depth. The difference between the crests and the depressions is about 8° F., with 12° as the greatest variation. . . . . Owing to the lagging of the soil temperatures, as compared with those of the air, the maximum is not attained until about 6 P.M., and the minimum about midnight.

A careful quantitative and qualitative investigation of the root relations of the lava inhabiting species is yet to be made, but it already gives promise of yielding some valuable contributions to our knowledge of plant ecology. To quote again from MACDOUGAL (*loc. cit.*, p. 82):

> It may be said, in conclusion, that the facts disclosed as to the actual temperatures in the soil, the diurnal and seasonal change therein, lead to the belief that the differences in temperature of the aerial and underground portions of plants cannot fail to be of very great importance in the physical and chemical processes upon which growth, cell-division, nutrition, and propagation depend. The determination of the effect of differences in temperature between the roots and aerial shoots has received but little consideration from the physiologist and the geographer.

Plant invasion on lava flows

The rate and amount of invasion is chiefly dependent upon two factors: (1) proximity of adjacent vegetated regions from which invasion may take place; (2) amount of precipitation, determining the character and abundance of invading forms. A lava flow which cuts a path through the humid jungle forest is soon (30–50 years) disintegrated and overgrown. A lava flow on an arid summit slope (8000–10,000 ft.) will remain practically naked for centuries. Between these two extreme types every intermediate stage can be found (figs. 11, 19, 20).

[12] CANNON, W. A., Root habits of desert plants, p. 20.

FIG. 19.—Floor of Kilauea, composed of black, lobular, hummocky *pa-hoe-hoe;* plants in foreground are *Metrosideros polymorpha*, *Vaccinium reticulatum*, *Sadleria cyatheoides*, etc.

FIG. 20.—Plant invasion on floor of Kilauea crater; near foot of wall; note that floor is smooth *pa-hoe-hoe;* ferns are *Sadleria cyatheoides;* scrubby trees near top of slope are *Metrosideros polymorpha*.

In 1912 FORBES[13] published some preliminary observations of plant invasion on lava flows. His principal findings, which coincide with the observations of the writer, may be summarized as follows:

1. Lichen flora is much more abundant on the *a-a* than on the *pa-hoe-hoe* and develops on the former at a much earlier date than the latter, other conditions being the same.

2. Ferns (such as *Polypodium* and *Sadleria*) and phanerogams (such as *Metrosideros* and *Sophora*) do not establish themselves upon the *a-a* until long after they have established themselves upon the *pa-hoe-hoe*, other conditions being the same.

3. The species occupying a recent flow are the same as those occupying older flows in the immediate vicinity.

4. Soil is formed on the *pa-hoe-hoe* at a much earlier date than on the *a-a*.

5. *Acacia koa*, a phyllodious species adapted to semi-xerophytic conditions, is the prevailing tree in the leeward upper forests of the middle zone, finally establishing itself upon the ancient flows as the dominant and final type.

Altitudinal ranges of lava flow species

Horizontal zonation with reference to altitude is strongly developed on the slopes of the Hawaiian mountains. As one ascends a great volcano like Loa or Kea, one finds pronounced changes in the vegetation with every thousand feet increase in elevation. From the standpoint of this paper the following large zones or belts may be recognized: lowland (littoral to 1500 ft.), lower forest (1000–2000 ft.), middle forest (1800–6000 ft.), upper forest (6000–9000 ft.), summit (9000–nearly 14,000 ft.). The summits of Kauai, Oahu, Molokai, West Maui, and Kohala rise to 4000–6000 ft. only and are very boggy. They are considered in another paper.[14] The point must be emphasized that there is a very considerable variation in the altitudinal limitations of these zones on the mountains of the different islands and on different slopes of the same mountain. In some regions the upper forest

[13] FORBES, C. N., Plant invasion on lava flows. Occ. Pap. Bishop Mus. 1912.

[14] MACCAUGHEY, VAUGHAN, Vegetation of the Hawaiian summit bogs. Amer. Bot. 22:45–52. 1916.

may cease at 6500 ft., in others the lower forest may extend almost to sea level; the figures must all be interpreted with considerable latitude for local deviation.

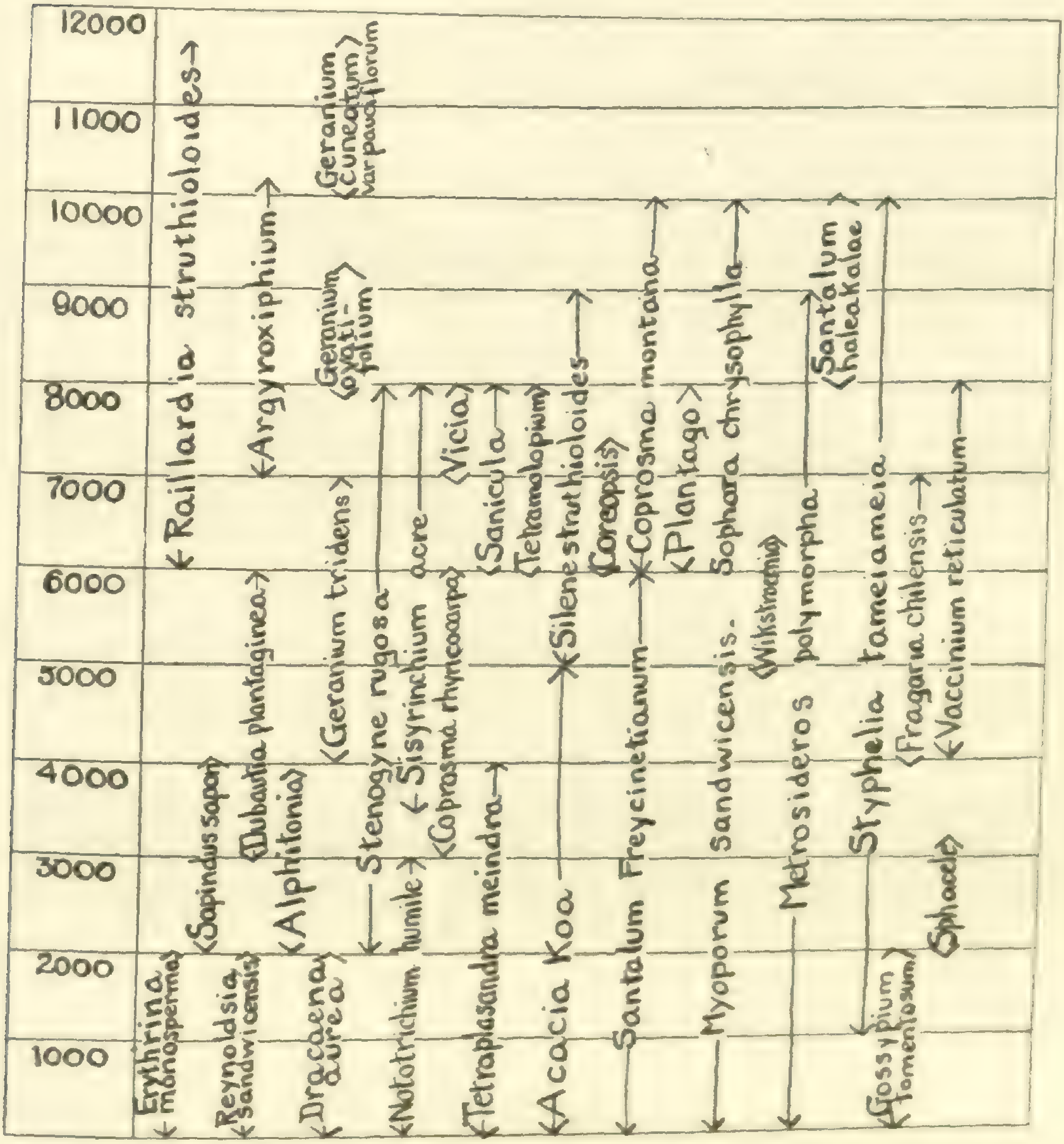

FIG. 21.—Diagram showing altitudinal ranges of some representative plants of lava flow country; figures indicate feet above sea level.

Upon classifying the lava flow species with reference to their altitudinal ranges (fig. 21), it is significant to note the great number of ranges and the fairly close adherence of each species to its range. Three general types of range may be cited: (1) wide-ranging species (*Metrosideros polymorpha*, *Sophora chrysophylla*, *Myoporum*

sandwicensis); (2) species with moderate range (*Charpentiera obovata*, *Daucus pusillus*, *Gossypium tomentosum*); and (3) species with a very narrow range (*Argyroxiphium virescens.*, *Geranium* spp., *Straussia* spp.).

Xerophytic characters of lava flow plants

PUBESCENCE.—Of the 182 species listed as occurring on the lava flows, 62, or 33 per cent, are characterized by coatings of hairy or woolly tomentum. The pubescence may cover the under surfaces of the leaves, the entire leaves, the young shoots, the inflorescences, or all aerial parts of the plant. The most pronounced examples of tomentose envelopment occur in the following genera: *Argyroxiphium*, *Gnaphalium*, *Chenopodium*, *Sida*, *Gossypium*, *Nototrichium*, *Waltheria*, *Abutilon*, *Geranium*, *Lobelia*, and *Plantago*. The point must be emphasized that with many indigenous Hawaiian plants there is exceeding variability as to pubescence; plants of the same species from various localities will show every gradation from perfectly glabrous to very hairy. This variation does not give evidence of intimate association with ecological habitat, although in a general way the glabrous forms characterize the rain forest and the pubescent forms the more arid situations. There are many exceptions to this rule, however, and a very considerable proportion of the pubescence seems to be without obvious ecological significance.

WAXY OR VISCID EXCRETIONS.—These are much less prevalent than the pubescent or coriaceous protections. Typical instances are *Argemone mexicana*, *Dodonea eriocarpa*, *Gardenia Brighami*, *Pisonia sandwicensis*, *P. inermis*, *Plumbago zeylanica*, *Raillardia* spp., *Sphacele hastata*, *Styphelia* spp., *Tetramolopium* spp., *Vaccinium* spp., *Myoporum* sp.

THORNS AND PRICKLES.—A small number of the lava flow plants are thorny or prickly; the condition characterizes introduced weeds rather than the indigenous vegetation, as shown by the following:

	Prickly	Thorny	Total
Indigenous	4	1	5
Introduced	4	5	9

Acacia Farnensiana, *Amaranthus spinosus*, *Argemone mexicana*, *Caesalpinia Bonducella*, *Cyanea solanacea* var. *quercifolia*, *Rubus hawaiiensis*, *Sida spinosa*, *Solanum incompletum*, *Opuntia tuna*, *Lantana camara*, and *Prosopis juliflora* are representative plants of this class (fig. 22).

FOLIAGE MINUTE OR SCALELIKE, or showing strong xerophilous modification.—*Acacia koa* and *A. koaia* (phyllodia), *Exocarpus Gaudichaudii*, *Portulaca sclerocarpa*, *Silene struthioloides*, and *Styphelia* spp. are examples of very small foliage. *Cassytha filiformis* and *Viscum articulatum*, two parasitic plants, have minute or vestigial leaves.

DECIDUOUS HABIT.—The deciduous habit is quite rare among Hawaiian plants, either in the rain forest or on the lava fields. Only 3 deciduous species occur on the lava flows, namely, *Erythrina monosperma*, *Sapindus saponaria*, and *Reynoldsia sandwicensis*.

DECUMBENT, STRAGGLING, OR VINELIKE HABIT.—A very large number, nearly 60 in all, or 33 per cent, of the lava flow plants are either habitually prostrate or decumbent, or assume these growth-forms on the lava. Genera containing representative species of these habits are *Abutilon*, *Argyreia*, *Boerhaavia*, *Caesalpina*, *Capparis*, *Cassia*, *Chenopodium*, *Cocculus*, *Embelia*, *Euphorbia*, *Fragaria*, *Gossypium*, *Ipomoea*, *Lepidium*, *Lipochaeta*, *Meibomia*, *Mucuna*, *Osteomeles*, *Plumbago*, *Portulaca*, *Raillardia*, *Ranunculus*, *Rubus*, *Rumex*, *Scaevola*, *Sicyos*, *Sida*, *Solanum*, *Stenogyne*, *Styphelia*, *Tetramolopium*, *Vicia*, *Vigna*, and *Wikstroemia*. Compact basal heads or rosettes are formed by such plants as *Argyroxiphium* spp., *Gnaphalium* spp., *Plantago pachyphylla*, *Sisyrinchium acre*, *Sonchus*, etc.

SUCCULENCE.—This typical xerophytic character is relatively uncommon in the lava flow flora. The few examples are mostly introduced weeds, as *Portulaca*, *Opuntia*, *Bryophyllum*, *Chenopodium*, *Sonchus*. Lignescence, representing the other extreme of structural adaptation to aridity, is the dominant condition.

HIGH PERCENTAGE OF LIGNEOUS FORMS.—Upon examining a tabular statement of the habital characters of the lava flow flora, one is immediately impressed by the high proportion of ligneous and semi-ligneous forms. Over 70 per cent are woody, and this

proportion would be heightened if a number of herbaceous perennials with woody bases or stocks were included. This ligneous character is not confined to the lava flow plants, however, nor is

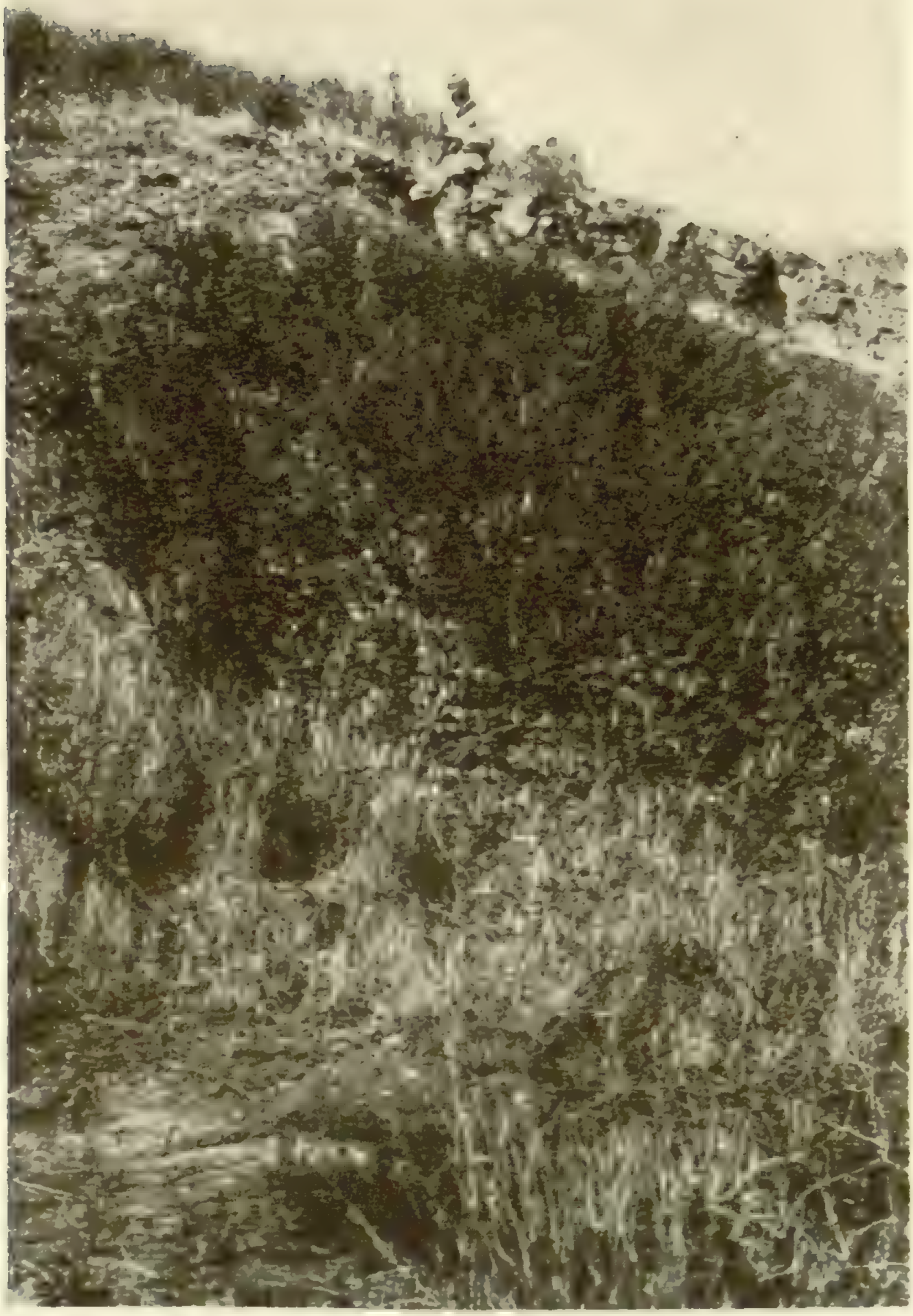

FIG. 22.—Typical ligneous thorny species dominant in xerophytic habitats, on lava flows and coastal plains, *Acacia Farnensiana;* man is standing on explosively produced tufa strata.

it especially typical of them. A very large proportion of the indigenous vegetation in the humid forests is shrubby or arborescent.

In the Hawaiian Islands woodiness is to be interpreted, not as a xerophytic feature, but rather as a result of long continued plant growth (in terms of the individual plant) under unfavorable conditions. The low temperatures and excessive humidity of the rain forest belt are probably just as unfavorable for optimum plant growth as are the high temperatures and excessive aridity of the lava fields. Both habitats result in the production or modification of a large number of very lignescent, suffruticose, dwarfed, slow growing species (tables I and II).

TABLE I

HABITAL ANALYSIS OF THE LAVA FLOW FLORA

Class	Frequent	Rare	Total
Trees	48	10	58
Shrubs	65	2	67
Herbaceous perennials	29	4	33
Annuals	24	2	26

TABLE II

ENDEMICITY AND LIGNESCENCE OF LAVA FLOW PLANTS*

Class	Endemic	Not endemic	Total
Woody throughout	90	18	108
Partly woody	28	10	38
Herbaceous	12	24	36
Total	130	52	182

*50 per cent of the total lava flow flora is composed of woody endemics; 80 per cent of the total lava flow flora is composed of woody and partly woody plants.

ROOT SYSTEMS OF LAVA FLOW PLANTS.—No comprehensive data are available on this interesting subject. The observations of the writer would tend to point to the comparatively deep rootedness of the woody species. The aridity of the flows has already been described. Deeply penetrating roots may be considered as absolutely essential for the existence of perennial plants on a rocky stratum as dry as the typical lava flow. The roots of such species

as the writer has had occasion to examine have in every case proved to be exceptionally long as compared with the proportions of the aerial parts. The roots run down for long distances into the fissures in the flows, and often pursue the most devious courses. The following plants exhibit this condition: *Acacia koa*, *A. Farnensiana*, *Alphitonia excelsa*, *Artemisia australis*, *Cassia Gaudichaudii*, *Cheirodendron Gaudichaudii*, *Coprosma montana*, *Dodonaea eriocarpa*, *Erythrina monosperma*, *Geranium cuneatum*, *Gossypium tomentosum*, *Lipochaeta subcordata*, *Metrosideros polymorpha*, *Myoporum sandwicensis*, *Osteomeles anthyllidifolia*, *Perrottetia sandwicensis*, *Psidium guayava*, *Reynoldsia sandwicensis*, *Rumex giganteus*, *Senecio vulgaris*, *Sida fallax*, *Sophora chrysophylla*, *Styphelia tameiameiae*, *Waltheria americana*, *Wikstroemia* spp., *Xylosma Hillebrandia*.

Sclerophyllous formations

A considerable proportion of the lava vegetation may be classified as sclerophyllous. The leaves of these species are thick coriaceous, usually with glistening, highly reflective upper surfaces. *Antidesma*, *Chrysophyllum*, *Coprosma*, *Maba*, *Metrosdieros*, *Nothocestrum*, *Osmanthus*, *Pelea*, *Pisonia*, *Pittosporum*, *Pterotropia*, *Sideroxylon*, *Styphelia*, *Wikstroemia*, and *Xylosma* are genera containing typical coriaceous-leaved species. It should be noted that Hawaii does not exhibit the extreme sclerophyllous condition, but rather a semi-sclerophylly. For example, many species with sclerophyllous foliage do not show noticeable dwarfing; indeed, they may be trees of considerable stature. In the Hawaiian Islands the sclerophyllous formations occur at the higher levels (5000–9000 ft.), and altitude seems to be a dominant factor in their origin and zonation.

AGE OF LAVA FLOW VEGETATION.—The vegetation of the lava flows is largely comprised of woody, long lived species. These acquire the aspect and habit of senility at a relatively early stage in their life cycles. The unfavorable conditions of the environment stamp themselves upon the physiognomy of the individual plants and of the formations as a whole. The woody species give every evidence of great age and slow growth. Shrubs 4–6 ft.

high show ages of 30 to 40 years; trees 15–20 ft. high, ages of 50 to 70 years; and trees of 40–60 ft. high, ages of 100 to 200 years or older. It may be stated as a general conclusion that the ligneous plants of the lava flows, like those of other deserts, attain great age and assume the aspect of senility at an early period in their lives.

Fossil trees

When a lava flow rolls down the mountain slope it may, and commonly does, meet with a grove or woodland across its path. The varying results of the encounter may be summarized as follows:

1. The forest may be entirely consumed by the lava flow, the trees beaten down and burned, and all trace of the grove wiped out by the rock sheet. This usually happens if the flow is *a-a* and is quite thick. There is abundant evidence on the slopes of Loa, Kea, and Haleakala to show that hundreds of thousands of acres of beautiful woodland have been obliterated by lava flows within comparatively recent geological time.

2. The flow, if of the *pa-hoe-hoe* type and moving quite rapidly through the grove, may only destroy the foliage, brushwood, and lesser vegetation. The large tree trunks are resistant even to the great heat of the flow. Moreover, the surface lava cools with such extreme rapidity (this is a noteworthy feature of the Hawaiian lavas) that the radiation from within is relatively slight. In this way large trunks are coated with an envelope or shell of lava which quickly cools and hardens, and forms a protective case, so that the heat from adjacent liquid lava does not reach the tree. The main mass of the lava flows on down the slope, leaving the grove spattered and jacketed with lava. Often great blobs of lava remain clinging to the larger limbs and festooning the summits of the saplings. Remnants of woodlands, exhibiting these phenomena, are not uncommon on the lee slopes of Loa.

3. The lava flow, acting under conditions like those just described, but moving more slowly, may ensheath the trees to a considerable height, for example, 20 ft. A jacket is formed as has been described, but the gradual incineration of the outer layer of wood results in a space between the tree trunk and the lava jacket. Fresh lava, under pressure, will force its way into this space, and

its heat will still further reduce the tree trunk. This process is continued until the tree is wholly consumed and the lava has filled the mold. The main flow passes on, leaving the lava trees behind. The result is a lava pillar or column, 15–25 ft. high, 2–5 ft. in diameter, and often expanded or flaring at the summit, where the trunk branched. These so-called "petrified trees" retain many evidences of their arboreal origin, and correspond somewhat in their mode of formation to the petrified trees of the west. In the Puna district, Hawaii, there are hundreds of these lava trees in the wake of ancient *pa-hoe-hoe* flows.

4. The fourth type of reaction between lava flow and woodland produces deep tubes instead of columns. The flow enters the grove and fills it to a depth of perhaps 20 ft. The rapid sheathing around the trunks of the larger trees protects them, as in the former cases, from immediate destruction. The flow in this instance, however, does not pass on and drain itself from the grove, but remains and solidifies. In the course of time the trunks decay and leave deep tubular vertical pits in the lava. The walls of these tubes are often plainly marked with the impressions of the bark of the trees which they once contained. The tubes are 10 in. to 5 ft. in diameter and 15–20 ft. deep. They are known as "tree molds," and are abundant on some of the old lava flows, particularly in the vicinity of Kilauea.

COLLEGE OF HAWAII
HONOLULU

SPEGAZZINIAN MELIOLA TYPES

F. L. STEVENS

(WITH PLATES XXIV–XXVI)

Through the kindness of Dr. CARLO SPEGAZZINI, I have received recently a number of original packages containing type specimens of *Meliola* described earlier by Dr. SPEGAZZINI. In each case the packet bore on the outside copious penciled notes concerning the specimen and careful, delicate drawings of the more significant structures. This collection of types, together with the notes and drawings in particular, are a fine commentary on the work of Dr. SPEGAZZINI. When we remember the large volume of his descriptive work and reflect that not only his types but other specimens as well are thus thoroughly and carefully annotated and figured, we are in a position more adequately to recognize the great indebtedness of mycology to him.

The drawings of the present collection have not been published, and in view of the comparative inaccessibility of most of these types, it is desirable that they should be made generally accessible to students by publication.

Permission having been received from Dr. SPEGAZZINI, Dr. ALVA PETERSON has faithfully copied for me, for publication, the most important of the drawings. Such copying was necessary, owing to the color of the paper upon which the originals were drawn, and the faintness of the penciling, which prohibited direct photographic reproduction. These drawings have been compared by me with the type material and are published herewith with such comments as seem necessary. A permanent celloidin mount[1] has been made from each specimen and, together with a fragment of the type specimen, is deposited in the herbarium of the University of Illinois. The original specimens have been returned to Dr. SPEGAZZINI at La Plata, Argentine.

MELIOLA ARMATA Speg. (fig. 1).—F. Puigg., Pug. I, no. 231; Sacc. 9:415.

[1] STEVENS, F. L., Phytopathology 6:367. 1916.

On coriaceous leaves, *Myrsine* (?), Apiahy, May 1888; no. 2382 (type).

The type specimen is heavily overgrown with several parasites. There is considerable variation in the character of the mycelium, which is sometimes straight, sometimes quite crooked. I have not been able to see the mycelial setae around the bases of the perithecia from which this species takes it name.

MELIOLA ARGENTINA Speg. (fig. 2).—Fung. Arg., Pug. I, no. 177; Sacc. 1:61.

On Cyperaceae, Buenos Aires, February 1880 (type).

The mycelium is very characteristic, close, dense, somewhat like *M. manca*, but distinguished by its very thick mycelial setae, which are striking, being darker and thicker than the mycelium. They are about 15 μ thick at base and over 800 μ long. The capitate hyphopodia are angular, that is, not smooth or echinulate as shown in fig. 2. The type is heavily overgrown by a *Coniothyrium.*

MELIOLA BRASILIENSIS Speg. (fig. 3).—Fung. Arg., Pug. IV, no. 116; Sacc. 1:66.

On leaves of Bignoniaceae (?), Apiahy; no. 1551 (type).

The young perithecia are surrounded by an areola of radiating hyphae. The perithecia also possess short hairs as figured and described by Dr. SPEGAZZINI.

MELIOLA CALVA Speg. (fig. 4).—F. Puigg., Pug. I, no. 233; Sacc. 9:414.

On Laurinaceae, Apiahy, August 1881 (type).

Heavily overgrown with "*Podosporium penicillium* Speg."

MELIOLA CLAVATISPORA Speg. (fig. 5).—F. Puigg., Pug. I, no. 241; Sacc. 9:422.

On leaves of Apocynaceae, Apiahy, April 1881; no. 1701 (type).

Perhaps the most striking character is in the sessile, nearly globular capitate hyphopodia.

MELIOLA CORONATA Speg. (fig. 6).—F. Guar., Pug. I, no. 175; Sacc. 9:428.

On *Luchea divaricata*, Guarapi, July 1883; no. 3847 (type).

The figure shows perithecial hairs to be more conspicuous than they usually are.

MELIOLA CRUSTACEA Speg. (fig. 7).—F. Puigg., Pug. I, no. 235; Sacc. **9**:413.

On *Drymis*, Apiahy, 1881 (type).

The mycelium forms a compact crustose colony, with the parts decidedly more crowded even than is shown in fig. 7.

MELIOLA DECIDUA Speg. (fig. 8).—F. Puigg., Pug. I, no. 240; Sacc. **9**:426.

On Convolvulaceae (?), Apiahy, April 1888; no. 2344 (type).

The capitate hyphopodia are very irregularly angular.

MELIOLA DELICATULA Speg. (fig. 9).—F. Guar., Pug. II, no. 63; Sacc. **9**:415.

On *Myrisinus*, Sierra de Peribebuy, September 15, 1883; no. 3985 (type).

MELIOLA ERIOPHORA Speg. (fig. 10).—F. Guar., Pug. II, no. 62; Sacc. **9**:413.

On *Ficus ibapoy*, Paraguay, January 1883 (type).

MELIOLA GLABRIUSCULA Speg. (fig. 11).—F. Aliq. Paul., no. 35; Sacc. **22**:48.

On Photiniae (?), Agua branca, Sao Paulo (type).

MELIOLA GLEDITSCHIAE Speg. (fig. 12).—Myc. Argent. VI, no. 1337.

On *Gleditschia amorphoidis*, Puerto Leon, Missiones, July 1909 (type).

MELIOLA GUAREAE Speg. (fig. 13).—Myc. Argent. VI, no. 1338.

On *Guarea balansa*, Puerto Leon, Missiones, August 1909 (type).

MELIOLA HARIOTI Speg. (fig. 14).—F. Guar. nonn. III, no. 78; Sacc. **11**:267; Gaill. Bull. Soc. Myc. Fr. **8**:186. 1892.

On Bignoniaceae, Paraguay, no. 1291 (type).

MELIOLA LEVIPODA Speg. (fig. 15).—F. Guar. nonn., no. 77 (p. 26); Sacc. **11**:264; Bull. Soc. Myc. Fr. **8**:181. 1892.

On *Aspidosperma quebracho*, Yaguaron, Paraguay, November 1882; no. 3589 (type).

MELIOLA LUDIBUNDA Speg. (fig. 16).—F. Guar. I, no. 178; Sacc. **9**:431.

On *Pilocarpus pinnatus*, Paraguay, January 1882; no. 3489 (type).

MELIOLA MEGALOSPORA Speg. (fig. 17).—F. Arg., Pug. IV, no. 115; Sacc. **1**:67.

On *Jodina rhombifolia*, January 1888 (type).

The very coarse hyphae are quite characteristic.

MELIOLA MELASTOMACEARUM Speg. (fig. 18).—F. Puigg., Pug. I, no. 232; Sacc. **9**:414.

On Melastomaceae, no. 2485, Apiahy, May 1888 (type).

The mycelium is often less straight than might be assumed from the figure. The oval hyphopodia are characteristic.

MELIOLA OBESA Speg. (fig. 19).—F. Guar., Pug. I, no. 179; Sacc. **9**:421.

On Rutaceae, Piragu Bras, July 1883; no. 3834 (type).

MELIOLA OBESULA Speg. (fig. 20).—F. Guar. nonn., no. 75; Sacc. **11**:262.

On Rutaceae, Caa-guaza, Brazil, January 1882; no. 3585 (type).

MELIOLA PUIGGARII Speg. (fig. 21).—F. Puigg., Pug. I, no. 228; Sacc. **9**:414.

On *Rubus*, Apiahy, May 1888; no. 2722 (type).

MELIOLA PULCHELLA Speg. (fig. 22).—F. Puigg., Pug. I, no. 227; Sacc. **9**:414.

On Myrtaceae, Apiahy, 1881; no. 1699 (type).

MELIOLA SAPINDACEARUM (fig. 23).—F. Guar. nonn., III, no. 79; Sacc. **11**:266; Bull. Soc. Myc. Fr. **8**:184. 1892.

On Sapindaceae, Caa-guazu, Brazil, January 1882; no. 3600.

MELIOLA SPEGAZZINIANA Wint. (fig. 24).—F. Guar., Pug. II, no. 64; Sacc. **9**:418.

On Compositae, Paraguari, March 5, 1883; no. 3751 (type).

MELIOLA SORORCULA (fig. 25).—F. Puigg., Pug. I, no. 230; Sacc. **9**:418.

On *Baccharis pingrea*, Apiahy, May 1886; no. 2774 (type).

MELIOLA SUBCRUSTACEA Speg. (fig. 26).—F. Puigg., Pug. I, no. 236; Sacc. **9**:430.

Apiahy, 1888; no. 2703 (type).

MELIOLA TABERNAEMONTANAE Speg. (fig. 27).—Myc. Argent. VI, no. 1345; Bompland Missiones.

STEVENS on MELIOLA

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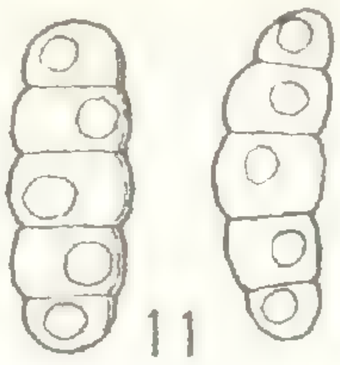
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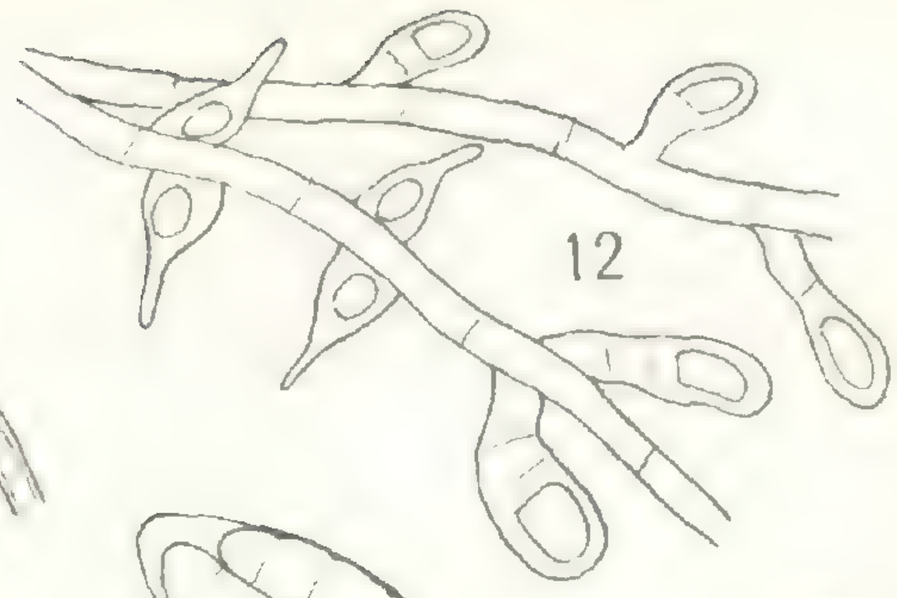
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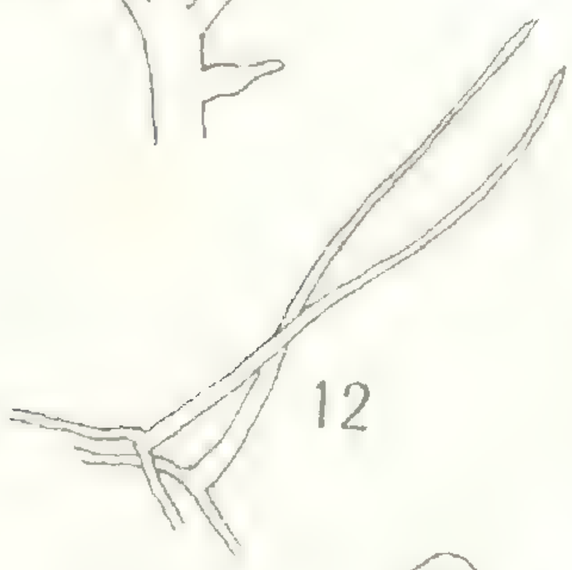
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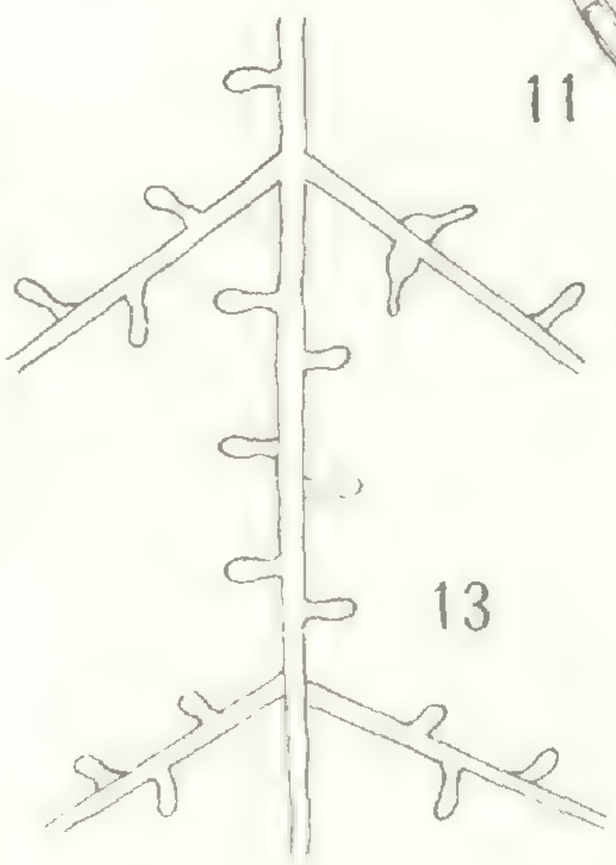
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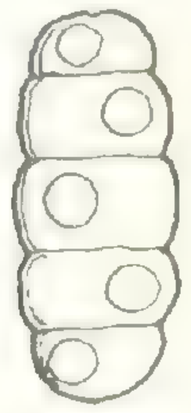
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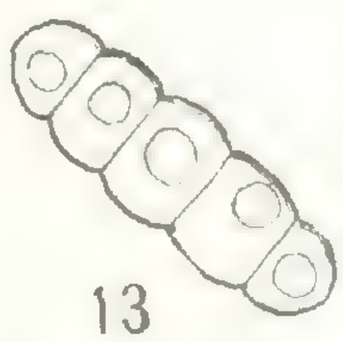
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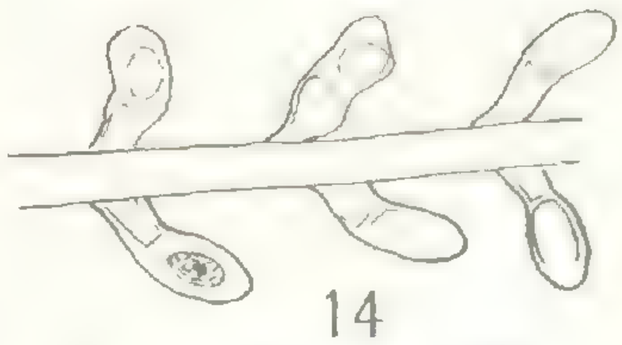
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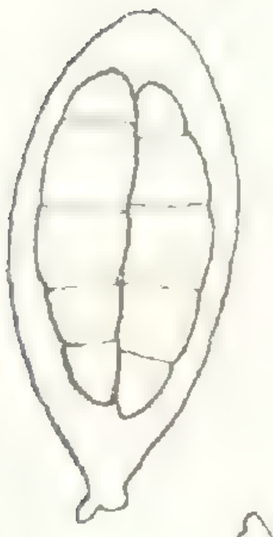
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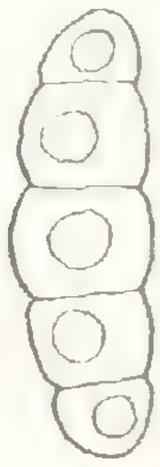
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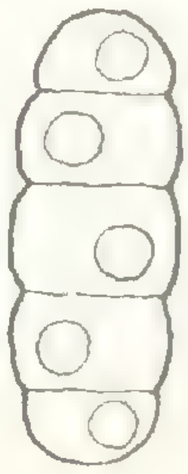
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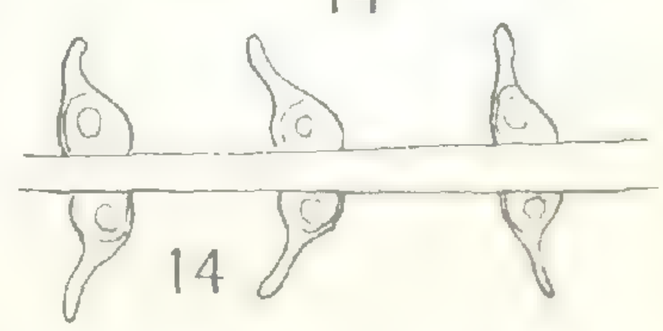
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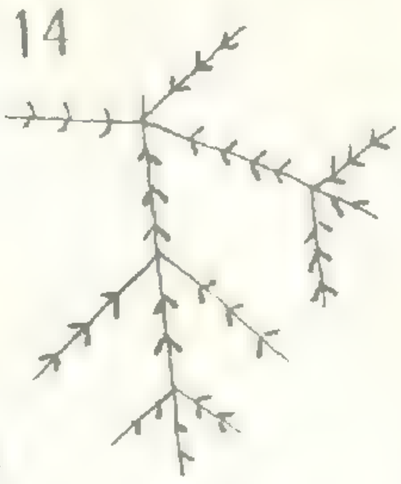
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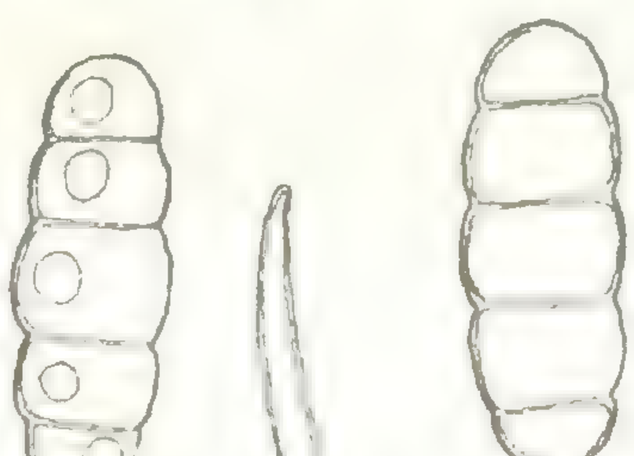
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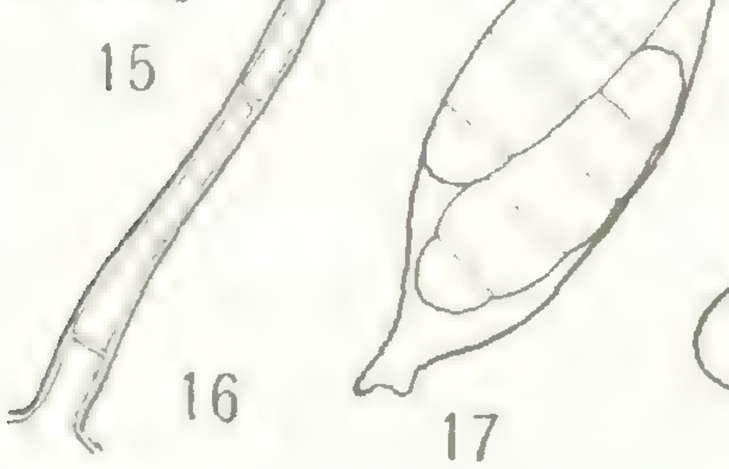
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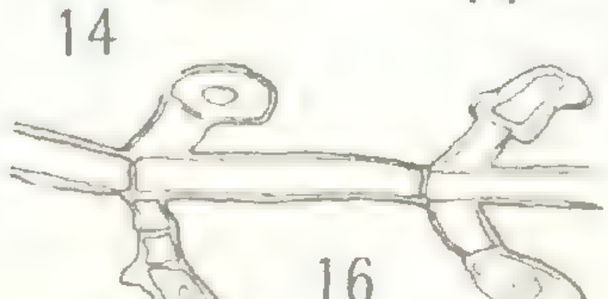
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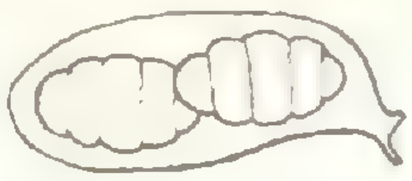
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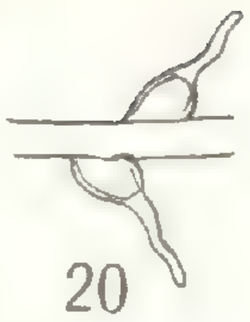
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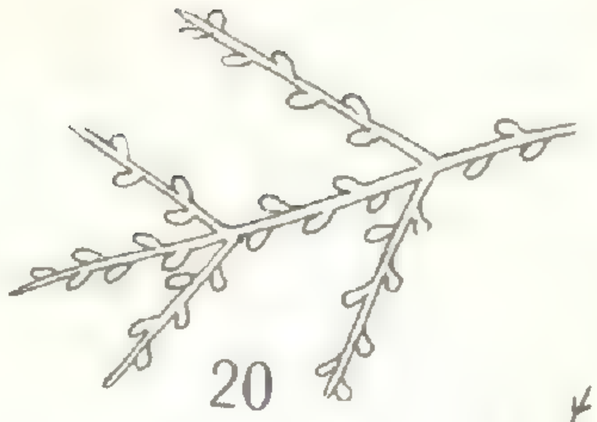
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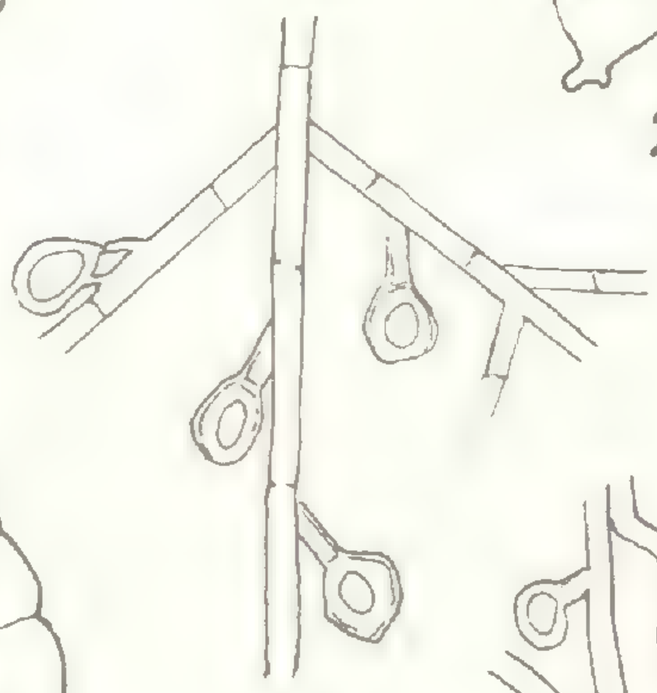
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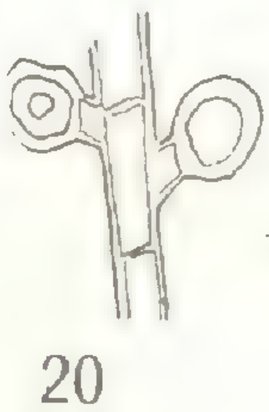
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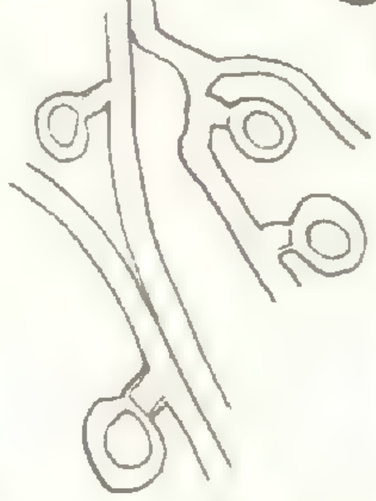
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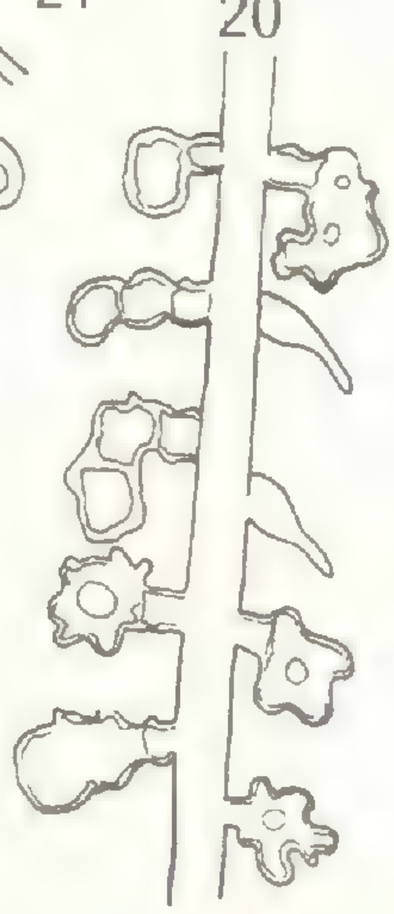
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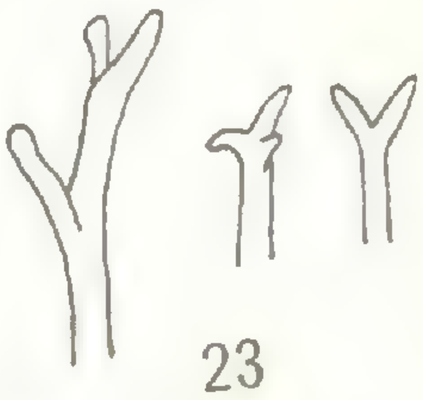
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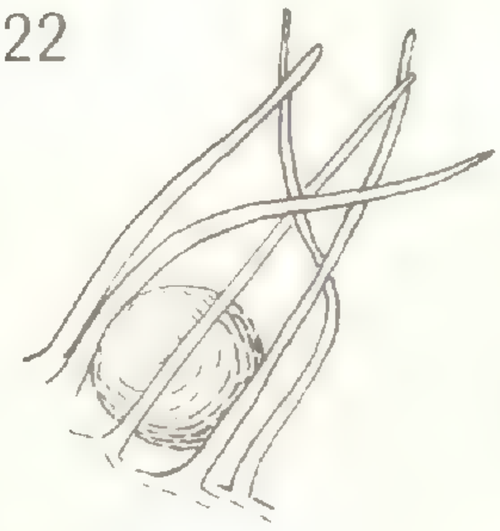
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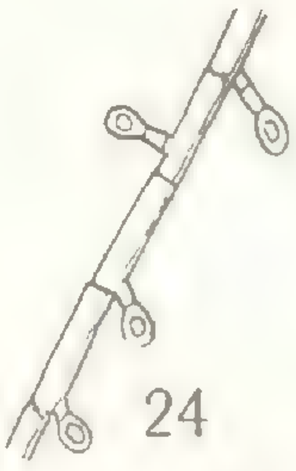
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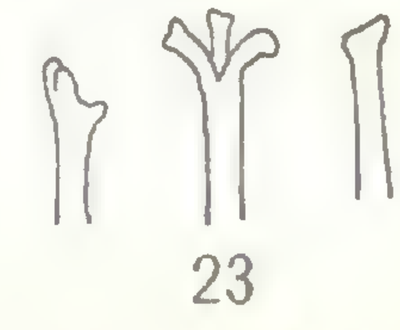
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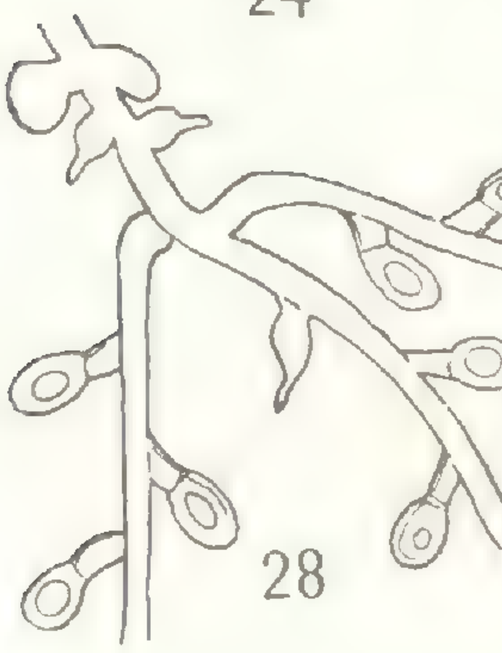
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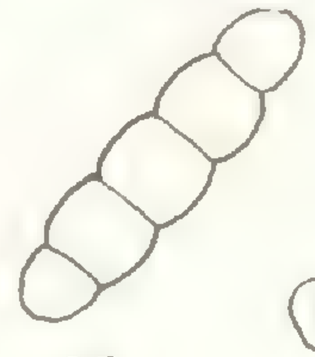
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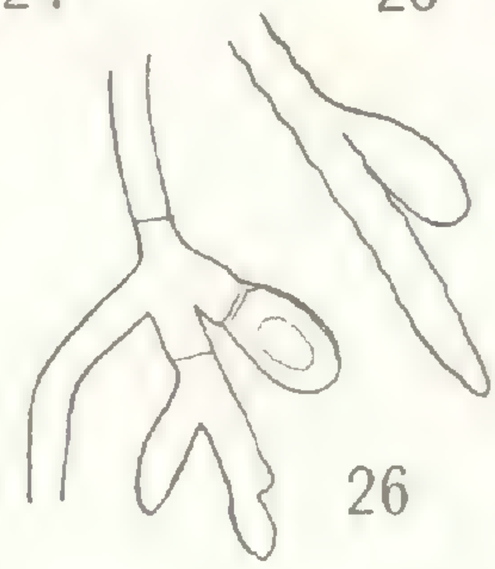
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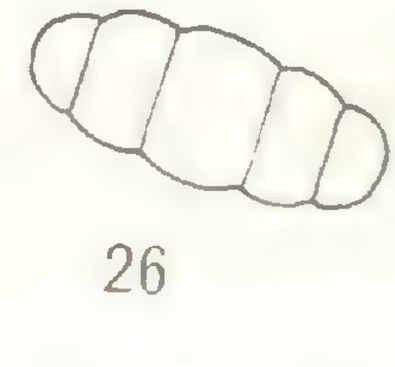
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STEVENS on MELIOLA

On *Tabernaemontanae historicis*, November 1909 (type).

MELIOLA TREMAE Speg. (fig. 28).—Myc. Argent. VI, no. 1346.

On *Trema micrantha*, Puerto Leon, Missiones, July 1909 (type).

MELIOLA GUARANTICA Speg. (fig. 29).—F. Guar., Pug. I, no. 176; Sacc. **9**:429.

On leaves of Guarapi, January 1883; no. 3681.

This species has been united with *Meliola ganglifera* by GAILLARD.

MELIOLA WINTERII Speg. (fig. 30).—F. Guar., Pug. II, no. 53; Sacc. **9**:424.

On *Solanum verbascifolium*, Sierra de Peribebuy, September 15, 1883; no. 3896 (type).

ABBREVIATIONS OF PUBLICATIONS CITED

Bull. Soc. Myc. Fr. = Bulletin Société Mycologique de France.

F. Puigg. = Fungi Puiggariani. Pugillus I. Boletine de la Academia Nacional de Ciencias de Cordoba. T. XI. Buenos Aires. 1889.

Myc. Argent. = Mycetes Argentinensis. I–VI. Anales de Museo Nacional de Historia Natural de Buenos Aires. 1902–1912.

F. Guar. = Fungi Guaranitici. Pugillus I and II. Analese de la sociedad Cientifica Argentina. 1883–1888.

F. Aliq. Paul. = Fungi Aliquot Paulistana. Revista del Museo de La Plata **15**:1908.

Fung. Arg. = Fungi Argentini, novi vel critici. Pugillus I, IV. Ann. Mus. Nacion. Buenos Aires. 1880–1882.

F. Guar. nonn. = Fungi Guaranitici nonnulli novi v. critici. Buenos Aires. 1891.

Sacc. = Saccardo, Sylloge Fungorum.

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STARCH FORMATION IN ZYGNEMA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 238

HELEN BOURQUIN

(WITH PLATE XXVII)

Between 1880 and 1895 much literature on the subject of starch formation appeared. At that time certain problems in regard to the origin of starch grains in algae arose which have not yet been settled. The present investigation of *Zygnema* was undertaken because its chromatophore appears to be typical of many algae, and it is so large that the possibility of error in cytological work should be minimized.

History

The most important investigations on starch formation were made by MEYER (3, 4). One of his conclusions is that starch is always formed by the plastid by secretion. Although he confined most of his attention to angiosperms, he believed this to be equally true for algae (4). He concludes that the pyrenoid is reserve protein material which is formed by the plastid and is used by the cell after its supply of starch has been exhausted. In his opinion it is homologous with the protein crystals formed in the plastids of many of the lower monocotyledons, which are likewise utilized after all the starch grains have disappeared. The plastid itself he sees as a colorless or slightly yellowish honeycombed structure ("vakuolig-poröse"), which contains chlorophyll in the form of granules. Other investigators agree that the pyrenoid is implicated in some way in the formation of starch in algae.

SCHMITZ (7) finds a specific pyrenoid substance which is laid down locally in the substance of the plastid in such quantities that the mass appears as a structure more or less sharply differentiated from the plastid. Although formed by the plastid, this pyrenoid substance is living and takes an active part in starch formation. He adds that in many cases the plastid forms starch without the intervention of the pyrenoid, and that pyrenoids often appear in

plastids in which no starch is formed. He thinks that the pyrenoid is homologous with the protein aleurone crystals of the lower monocotyledons, and he places the pyrenoid substance in the same chemical group as chromatin.

SCHIMPER (5, 6) describes the pyrenoid as a crystalline substance which rises *de novo* in the cytoplasm, and which in turn gives rise to the sheath of starch grains surrounding it. The plastids of algae always form it in the process of starch formation. If abundant, it crystallizes; if thin, it passes into starch without crystallizing and its presence cannot be demonstrated by the microscope, as is possible when it is in crystalline form. It and its surrounding sheath of starch grains are structures peculiar to algae and not homologous with any structures found elsewhere in plants. He believes that it does not belong to the same group as chromatin.

According to TIMBERLAKE (8) there is no differentiated chromatophore in *Hydrodictyon utriculatum*, but the chlorophyll is distributed through the whole peripheral protoplasmic layer of the cell (p. 623). Just before zoospore formation the pyrenoids disappear. They rise *de novo* when the zoospores germinate. The substance of the pyrenoid is changed into starch grains by "processes not understood." He is inclined to believe that the pyrenoid is an active independent cell organ whose function is to produce starch.

YAMANOUCHI (9) finds a plastid in *Hydrodictyon africanum*, a plant like *H. utriculatum* in all essential features. In its early stages the plastid is denser in the outer regions than in the center and is irregular platelike or spindle-like in form. It may produce either reserve starch grains or pyrenoids. The two are not recorded in the same plastid.

CHMILEWSKIJ (1) believed that the starch grains in *Zygnema* are formed wholly from the substance of the pyrenoid, plates of which extend between the starch grains, giving a starlike structure.

Miss MERRIMAN (2) figures the starch grains as entirely surrounded by cytoplasm except on the side abutting on the pyrenoid. Since this work of Miss MERRIMAN's has been accepted as the standard on nuclear division in *Zygnema*, it seems necessary to emphasize the fact that she makes no claim of having interpreted

the chromatophore correctly. She has figured it incidentally as it appears to the casual observer.

Material and methods

My observations were made on several species of *Zygnema*. The material came from the vicinity of Chicago and from Dr. TRANSEAU'S laboratory. It was killed in 1 per cent chromoacetic acid, part of it at 11:00 P.M. to secure cells which were dividing, and part of it at 11:00 A.M. to catch the cells in an active vegetative condition.

Filaments were mounted whole in Venetian turpentine and stained with anilin blue and Magdala red and with gentian-violet and anilin blue in order to differentiate the parts of the chromatophore. Iron hematoxylin was also used for some preparations. Most of my observations were made on the whole filaments. Many of the drawings are optical sections of whole chromatophores. The advantage in this method lies in the fact that the true sizes and relations of the starch grains and the exact extent of the pyrenoid in the chromatophore can be ascertained by focusing up and down. The use of sectioned material exclusively might lead to errors of interpretation by taking the transverse section of a grain for a small one, or by failure to see the full extent of the pyrenoids. Longitudinal and cross-sections of cells 3 μ thick were also made and were stained with gentian-violet and safranin, iron hematoxylin, and Flemming's triple stain. An 8× ocular and a 2 mm. objective were used for examining the preparations.

I wish to thank Dr. C. J. CHAMBERLAIN for much valuable help and for his many suggestions.

Description

The chromatophores lie, one on each side of the nucleus, in the middle of the cell, suspended there by means of bands of cytoplasm which radiate from them to the layer of the cytoplasm along the cell wall (fig. 1). Under low-power lenses these bands appear to be part of the chromatophore and have led writers of textbooks to speak of the star-shaped chromatophore of *Zygnema*. The chromatophore is really round or oval in shape. It is a plastid containing imbedded in its substance a pyrenoid, which lies near

the center, and starch grains which radiate out from the pyrenoid (fig. 7).

Staining differentiates the plastid from the pyrenoid and the starch grains. The plastid is stained a bright blue by anilin blue, gray by iron hematoxylin, and faintly violet by gentian-violet when the starch grains are stained very deeply violet. It is colorless when the starch grains are only faintly violet. The latter are stained a yellowish red by Magdala red and violet by gentian-violet. The pyrenoid stains red with Magdala red and safranin and dark blue with iron hematoxylin. The plastid is differentiated from the cytoplasm which surrounds it by its structure, the plastid appearing homogeneous (figs. 1, 7).

It is most easily seen in chromatophores which are dividing (figs. 17, 18), but any chromatophore in which the starch grains are not closely packed shows it. A layer of the substance of the plastid always surrounds each starch grain and the pyrenoid, thus separating the starch grains from each other and from the pyrenoid. This layer can be demonstrated even when the starch grains are most closely packed (figs. 1, 2, 3, 10).

The pyrenoid is a homogeneous structure which stains with different intensity in different parts of its mass, so that one part of it will be dark blue and another gray, or one part lighter red than another. It usually forms a compact, irregularly oval or round mass in the center of the plastid from which it is sharply differentiated. An examination of the figures will show that it may vary greatly from these shapes, but it does not extend up between the starch grains as CHMILEWSKIJ (1) believed. Staining the chromatophore with Magdala red, which stains the pyrenoid, and with anilin blue, which stains the plastid, proves this conclusively. Occasionally, when there is a large space between two starch grains, tongues of the pyrenoid extend a short way up between them (fig. 8). These tongues never reach the periphery of the plastid, come into direct contact with a starch grain, or surround one.

I have not found more than one pyrenoid in a plastid unless that plastid was about to divide, division of the pyrenoid always immediately preceding the division of the plastid (figs. 17, 18).

In the majority of chromatophores the starch grains lie radially about the pyrenoid, with their broad end toward the periphery of the plastid and the narrow end abutting on the pyrenoid (figs. 1, 2, 10). They are approximately equal in length, but vary in shape from cuneate to trapezoidal to rectangular (grains *l*, figs. 2, 3, 10, 16). Their opposing faces are straight; the outer faces are rounded or straight.

In many plastids there are minute grains in the periphery of the plastid (figs. 8, 10, 15, 16). Grains of all sizes from minute grains to the larger grains are also found. These intermediate grains are all cuneate in shape, if they lie between the larger grains, and always occur near the periphery of the plastid (figs. 8, 15, 16). Occasionally the starch grains are clustered irregularly about the pyrenoid (figs. 8, 15). In this case also the smaller grains are found in the periphery of the plastid.

Discussion

There are two opinions about the origin of starch grains in algae. The majority of investigators believe that the pyrenoid is concerned in starch formation. MEYER believes that the pyrenoid is not concerned in starch formation. The pyrenoid may be implicated in starch formation in either of two ways. Its substance may be changed into starch, that is, it may form starch by fragmentation, as SCHIMPER (**5, 6**) and TIMBERLAKE (**8**) believed, or it may be an active starch-former by secretion.

In *Zygnema* the substance of the pyrenoid is not changed into starch. This is shown by a comparison of the shape and position of the starch grains and the shape and position of the pyrenoid and by an examination of the pyrenoid itself. If the starch is formed by fragmentation of the pyrenoid, there should be such a similarity in the contour of the two that the starch grain could be fitted into the edge of the pyrenoid as the parts of a puzzle fit together. If the grains are chipped out so that they come to lie radially about the pyrenoid, bands of the pyrenoid should lie between the starch grains. Even though the pyrenoid were to grow and change shape after the formation of each starch grain,

some newly formed grains would always be found which would indicate their origin in that way.

Typically the pyrenoid forms a round mass in the center of the plastid (fig. 1). The most extreme variations in its shape are figured (figs. 2, 8, 12, 14). In no case is there a striking similarity between the contour of the pyrenoid and the starch grains, nor does the pyrenoid extend between the starch grains in such a way as to suggest that the starch grains have been cut out of the substance of the pyrenoid. Fig. 8 is the most suggestive found.

Although the pyrenoid is stained with different intensity in different parts, the whole pyrenoid stains the same color with any given stain. The narrow band of the substance of the pyrenoid connecting the halves of a dividing pyrenoid never stains deeply (fig. 18). In the vegetative plastid these light and dark areas bear no definite relation to each other or to the surrounding starch grains (figs. 2, 3, 8, 9, 11, 15). Moreover, these light and dark areas are uniformly homogeneous in structure. I believe, therefore, that they do not indicate any change in the substance of the pyrenoid; they are simply regions of different density.

Grains lying radially about the pyrenoid and varying in shape from cuneate to rectangular might be formed by the pyrenoid by secretion were the pyrenoid to form them in the periphery of the plastid and add to them centripetally, or to form them at the center of the plastid and add to them continually on the inner edge, such additions pushing them automatically toward the periphery of the plastid. The first manner of formation is impossible since the pyrenoid is always confined to the center of the plastid and in no case was seen to approach the periphery where the smaller grains of starch occur. The nearest approach to such a situation is seen in figs. 8, 14. The second possibility cannot exist because the small grains are never found next to, or near, the pyrenoid. They were found without exception in the periphery of the plastid. Since there is no indication that starch grains ever split, they could not have been derived indirectly from the pyrenoid in that way. The fact that the plastid separates the pyrenoid and the starch grains becomes significant when added to these proofs that the pyrenoid does not take part in starch formation in *Zygnema*.

Everything bears out the following theory concerning the origin and growth of the starch grains in the form. The plastid gives rise to minute starch grains in its periphery, either between the larger grains (figs. 15, 16) or entirely beyond them (figs. 8, 11). Their growth seems to be regulated by their position in relation to the larger grains and to be a mechanical matter. Figs. 5, 6, 13 show how the shapes of the grains seem to fit naturally into the place occupied. If the small grains lie between larger grains, the plastid adds to them in such a manner that they become cuneate in shape. The enlargement on the inner face continues to be more rapid lengthwise of the grain than laterally as it grows down between the grains toward the center of the plastid, so that when it attains the length of the large grains it is still cuneate. A comparison of grains *t* in figs. 3, 8, 14, 16 shows a complete gradation in the lengths of the grains from the shortest to the longest, so that a perfect series could be arranged were the grains removed from their respective plastids.

After lengthening the grain in the manner described, the plastid begins to add most rapidly to the narrow base laterally, so that the grain becomes trapezoidal and then rectangular in shape. In rare instances this basal broadening may continue until the grain is once more trapezoidal (fig. 2). Grains *l* in figs. 2, 10, 16 show every stage in the change of shape just mentioned. If the small grains are formed above larger grains, they grow rectangular or oval, pushing the grain below toward the pyrenoid. This is the unusual rather than the normal method of growth, however.

Summary

The chromatophore of *Zygnema* is a plastid containing imbedded in its substance a pyrenoid which lies near the middle, and starch grains which usually lie radially about the pyrenoid.

The pyrenoid cannot take part in starch formation because it is always confined to the center of the plastid and is separated from the starch by the plastid, and because the small young grains of starch are always found in the periphery of the plastid. The plastid therefore must form these minute starch grains.

The starch grains come to lie radially about the pyrenoid in the following manner. The plastid adds to them in such a way that they become cuneate in shape. In this manner they grow down between the starch grains already formed until they are of the same length as the large grains. The plastid then broadens them at the base until they become rectangular in shape.

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EXPLANATION OF PLATE XXVII

The drawings were made by the aid of the camera lucida, the magnification being ×1040. The abbreviations used are as follows: *c*, cytoplasm; *r*, pyrenoid; *n*, nucleus; *p*, plastid; *g*, starch grain; *t*, starch grain growing in length toward center of plastid; *l*, starch grain growing broad at base; *s*, minute starch grain.

FIG. 1.—Optical section of cell showing relation of cytoplasm, nucleus, and chromatophores, and showing typical chromatophores packed with large starch grains radiating from pyrenoid.

FIG. 2.—Optical section of chromatophore showing grains of varying width at base.

FIG. 3.—Optical section of chromatophore showing grains of varying lengths and grains which vary in width of base as compared with width of outer edge.

FIG. 4.—Cross-section of chromatophore showing grains of starch in cross-section.

FIG. 5.—Same as fig. 4.

FIG. 6.—Same as fig. 4.

FIG. 7.—Optical section of chromatophore showing several smaller starch grains in periphery of plastid.

FIG. 8.—Optical section of chromatophore showing minute starch grains in periphery of plastid, a pyrenoid of unusual extent and shape, and many starch grains which vary greatly in shape and length.

FIG. 9.—Median longitudinal section of chromatophore showing several small starch grains.

FIG. 10.—Same as fig. 2.

FIG. 11.—Cross-section of cell showing chromatophore in cross-section.

FIG. 12.—Same as fig. 9.

FIG. 13.—Same as fig. 9.

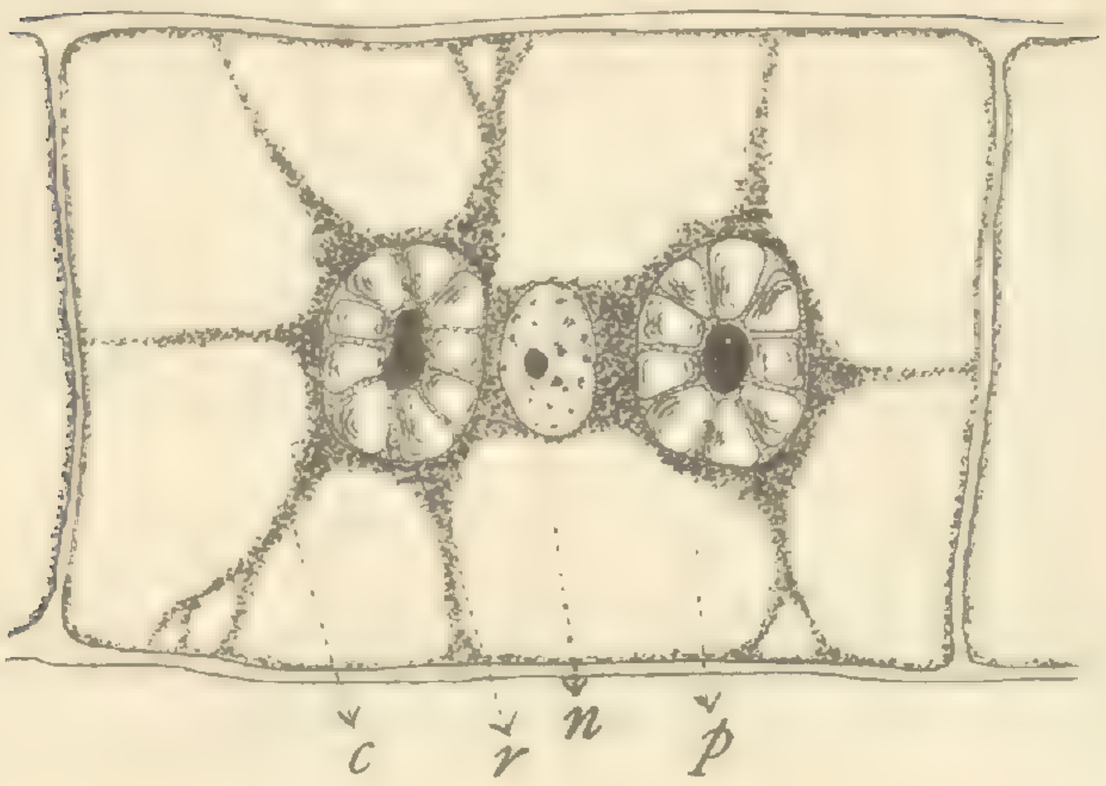
FIG. 14.—Optical section of chromatophore showing another pyrenoid of unusual shape, and starch grains of several different lengths.

FIG. 15.—Optical section of chromatophore showing many small starch grains near periphery of plastid, and large grains which differ in shape because of width of bases.

FIG. 16.—Same as fig. 15.

FIG. 17.—Optical section of plastid in process of division, showing pyrenoid after it has divided.

FIG. 18.—Optical section of plastid in process of division before pyrenoid has completed division.



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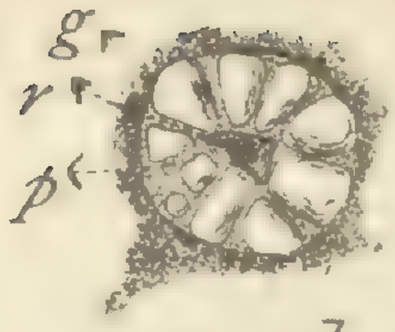

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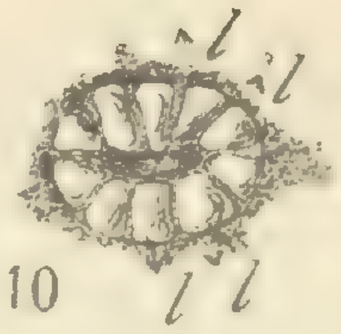

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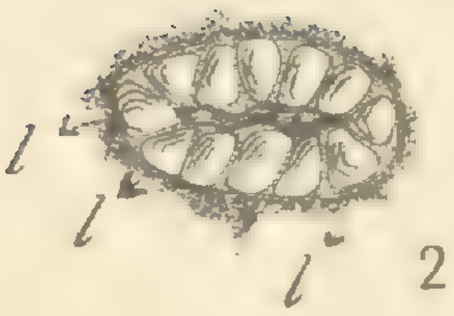

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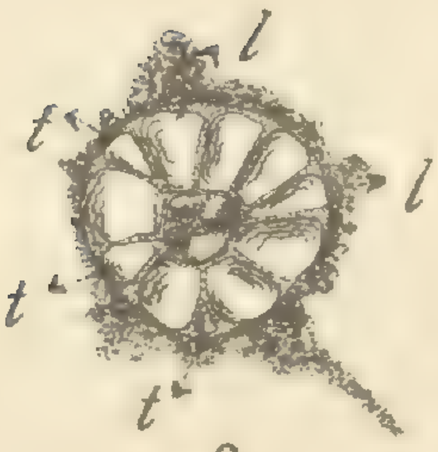

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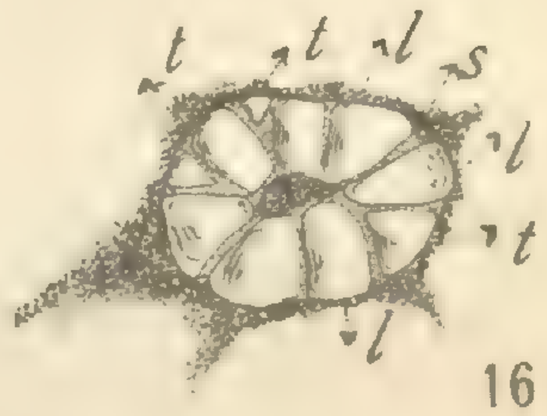

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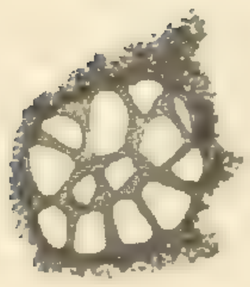

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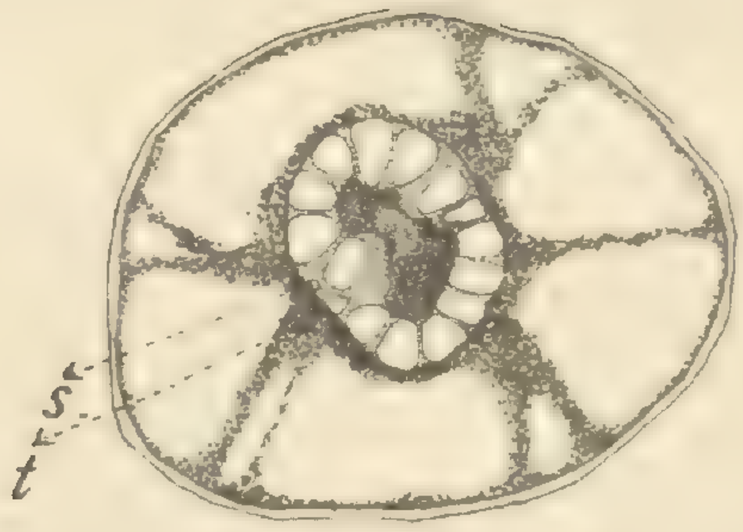

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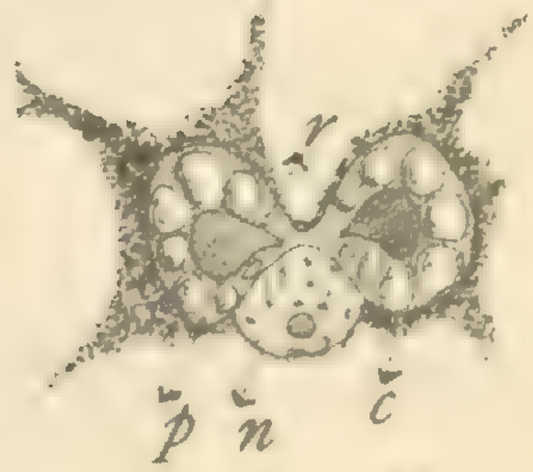

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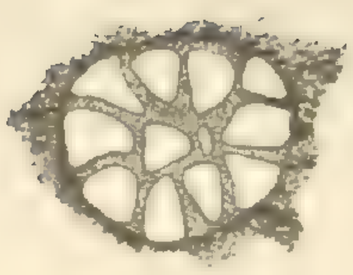

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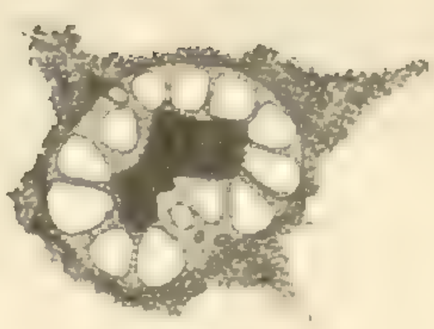

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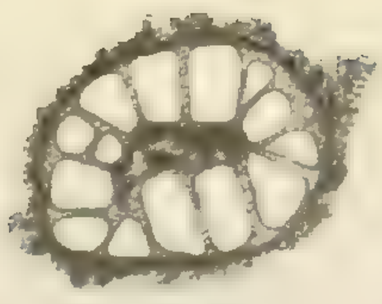

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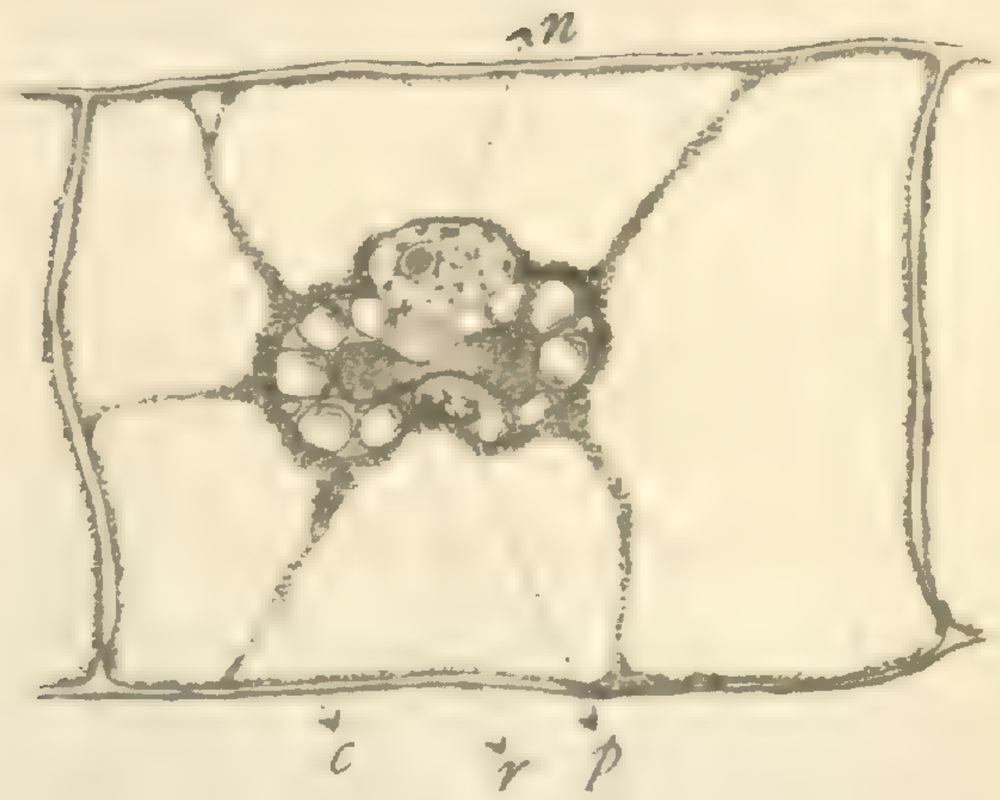

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BOURQUIN on ZYGNEMA

BRIEFER ARTICLES

APOGAMY IN PHEGOPTERIS POLYPODIOIDES FÈE, OSMUNDA CINNAMOMEA L., AND O. CLAYTONIANA L.

Apogamous embryos developed on prothallia of *Phegopteris polypodioides* Fèe, *Osmunda cinnamomea* L., and *O. Claytoniana* L. in cultures on Prantl's and Knop's full solutions and certain modifications of the Prantl's solution. About 6 months after the spores had been sown, the first cases of apogamy were observed in cultures of *Phegopteris polypodioides* on Prantl's solution with $NH_4 NO_3$ omitted. The spores from which the prothallia developed had been collected during the summer from a plant growing on a lawn in Ithaca, New York. The plant did not appear in a normal, healthy condition, doubtless owing to the unfavorable conditions under which it was growing. After the spores were sown upon the nutrient solutions, the cultures were placed before an east window, where the conditions of light and temperature were approximately the same for all. Once each week the prothallia were transferred to fresh nutrient solutions.

The prothallia, upon which the apogamous embryos developed, were heart-shaped and developed archegonia but no antheridia. The apogamous embryo in most cases originated as a slight swelling of the archegonial cushion, either on the dorsal or ventral side, at some point near the notch or at the center of the cushion. This swelling gradually increased until a dome-shaped cellular mass was formed, from which the apogamous embryo developed. The parts of the embryo usually appeared in the following order: the leaf or leaves, root, and stem. However, in one case a root appeared before any other member. No foot was formed. In some cases, beside leaves, proliferations, either filamentous or slightly expanded at the apices, developed from the cellular mass. October 7, 1916, two series of cultures on the Prantl's and Knop's full nutrient solutions and modifications of the Prantl's solution were made. Fresh spores from the same plant at Ithaca, New York, as well as spores of the same species secured through the kindness of Dr. A. H. Graves from Brooklin, Maine, were used. As soon as the spores were sown upon the nutrient solutions, one series was placed in the greenhouse in bright light, while the other series was kept in the laboratory before an east window. The prothallia were not transferred to fresh solutions, but

were allowed to remain upon the original solution on which the spores had been sown. A luxuriant growth of algae developed in all of the cultures, which added to the unfavorable growing conditions.

March 9, 1917, in both series of cultures, apogamous embryos were observed on the prothallia which developed in Knop's full solution from spores collected in Maine. Archegonia were developed on many of the heart-shaped prothallia, while in some of the cultures on the smaller prothallia antheridia were present. Some of the archegonia appeared aborted. In most cases the apogamous embryos developed in the manner which has previously been described. However, a few cases of peculiar development were observed. Multicellular hairs or outgrowths formed at the base of the first leaf or leaves of the young sporophyte, or at various places on it.

On one prothallium a long cylindrical outgrowth several cells in thickness developed from the cellular mass along with the leaves of the apogamous sporophyte. As growth proceeded, this outgrowth broadened out into a one-celled prothallium-like structure, after which it again assumed the cylindrical shape bearing tracheids; at its apex it tended to return to the prothallium structure. On another prothallium an outgrowth which had developed from the notch of the prothallium and projected as a narrow process broadened at the apex, forming a slightly notched prothallium.

The only cases of apogamy on prothallia developed from spores collected at Ithaca, New York, occurred in the culture of Knop's full solution which had been kept in the laboratory. Most of the apogamous embryos originated from cellular masses formed on the prothallia, but on one prothallium a cylindrical outgrowth bearing tracheids developed from the cells in the notch. At the apex of this long cylindrical process a cellular mass was formed, from which the leaves, root, and stem of the apogamous embryo developed.

Two series of cultures of *Osmunda cinnamomea* and *O. Claytoniana* were made at the same time, in the same manner, and placed under the same conditions as the cultures of *Phegopteris polypodioides*. Apogamous embryos were observed March 9, 1917, on the prothallia in the following solutions: Prantl's full solution, Prantl's solution with NH_4NO_3 omitted, and Prantl's solution with $MgSO_4$ omitted. Some of the apogamous embryos developed from cellular masses; others originated as cylindrical outgrowths containing tracheids, from the notch of the prothallia, bearing at their apices cellular masses which gave rise to the leaves, root, and stem of the sporophyte. On one prothallium an apogamous sporophyte formed near the notch, while at its base a lobe of the prothallium

developed, on which in turn occurred an apogamous embryo. In the latter the root developed first. Only three cases of apogamy were observed in *Osmunda Claytoniana* in Prantl's solution with K_2SO_4 omitted. In two cases the sporophytes developed from a mass of cellular tissue, while the third arose as an outgrowth in the notch of the prothallium. A further study will be made of these apogamous forms.—ELIZABETH DOROTHY WUIST, *Osborn Botanical Laboratory, Yale University.*

RAY TRACHEIDS IN QUERCUS ALBA

(WITH ONE FIGURE)

In the course of a recent study of the medullary rays of the Fagaceae, the writer was impressed with the manner in which some of the fibro-tracheids in *Quercus* were associated with the rays. It is very common

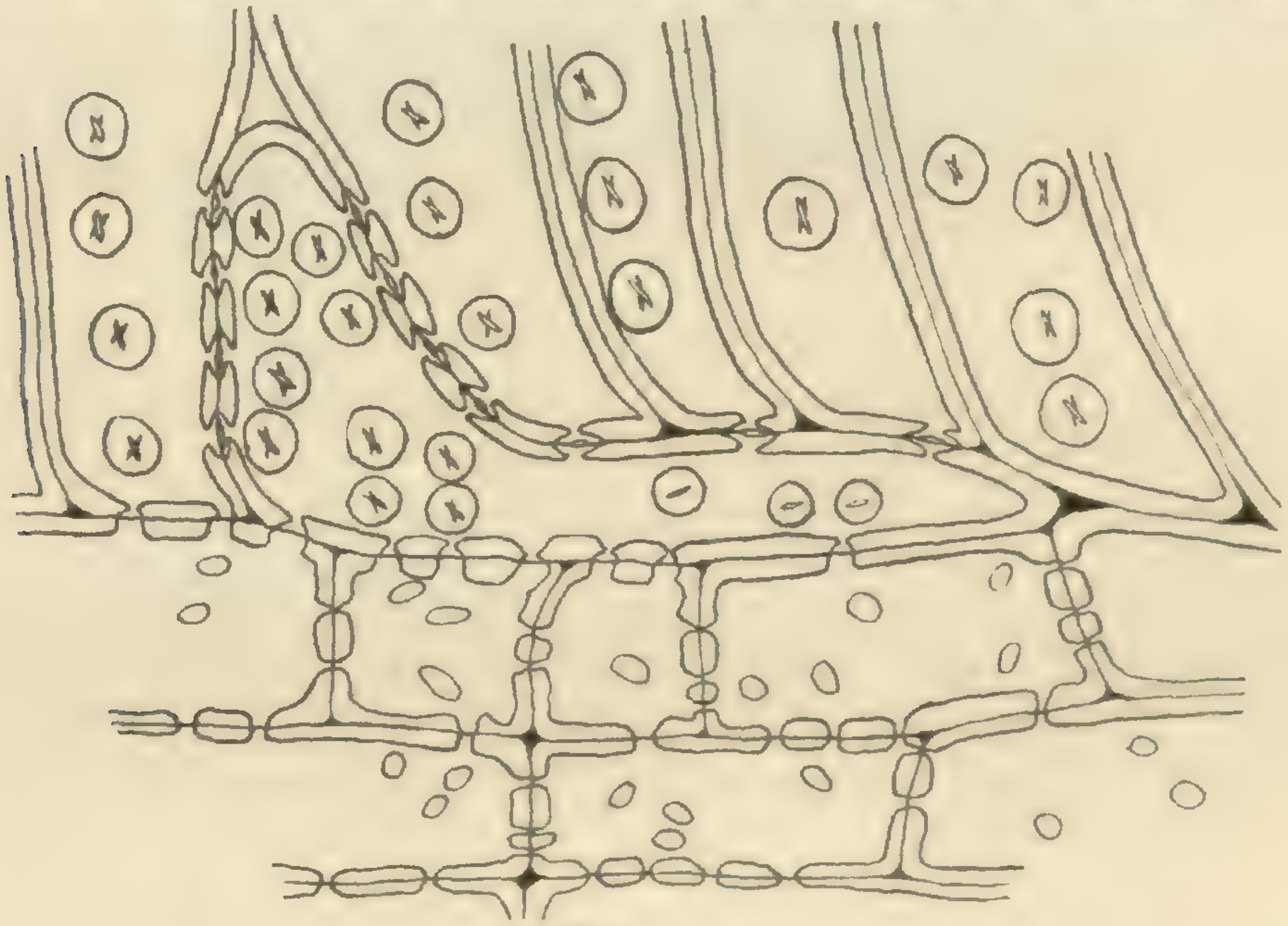

FIG. 1

to find the ends of these elements procumbent on the marginal ray cells for a considerable distance and communicating through semi-bordered pits. This condition is so similar to that found in certain coniferous woods that search was made in sections of oak wood at hand for tracheids that were distinctly radial. Fig. 1 shows a marginal ray tracheid of a uniseriate ray in normal stem wood of *Quercus alba* Linn. Another, somewhat smaller, was found in a different ray in the same section. The location is in the median late wood of the season's growth and is not in immediate proximity to a large vessel. So far as the writer is aware, ray tracheids have not previously been reported in the woods of the dicotyledons.—SAMUEL J. RECORD, *Yale University.*

CURRENT LITERATURE

BOOK REVIEWS

Physical chemistry and biology

McClendon[1] has performed a valuable service to biologists by organizing the more important facts and principles of physical chemistry that have to do with biological problems. These are stated briefly and concisely, and the usefulness of the book is increased by clearness in definitions. Several passages in the introduction are suggestive of helpful lines of work and interpretation.

The following paragraph from the preface suggests the viewpoint: "The purpose of this book is not to go far into physical chemistry, but to develop a tool for physiological research. Lengthy discussions of debated questions are avoided by tentatively accepting the hypothesis which fits the most facts, until a better one appears. For further discussion of any subject the reader is referred to the literature list and index. For facts, however, he is referred to nature. It is not to be hoped that theories should coincide exactly with data available at present. Even in the most exact branches of chemistry the atomic weight determinations, for instance, do not exactly coincide with the values calculated from the atomic numbers, and there seems to be some doubt as to whether lead is one element or several. How much more uncertainty there should be about physiology, where determinations are vitiated by the great variability of the material and its physiological states."

The book seems to be more from the biological standpoint and much better balanced than some other books on the relation of physical chemistry to biology that have come to the attention of the reviewer. In the introduction the author says, "Though the problems considered in this book are physiological, the methods of attack are chiefly those of the physical chemist." The book should do much toward encouraging the kind of work and thought that is neither distinctly chemical, in the sense of ignoring the structures and physical environment within which the reactions must take place in organisms, nor yet strictly biological, in the sense of ignoring any of the chemistry involved.

When the author states (p. 1) that the methods that may be applied to the interior of living cells are at present very few and concerned chiefly with the inorganic constituents, he is putting entirely too low an estimate on microchemistry as a means of investigation. It is true that this is as yet an imperfect tool, but still it is useful in a great many cases in detecting organic compounds as well as inorganic. While his statement that "modern biochemistry is therefore not yet concerned directly with the composition of normal living

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[1] McClendon, J. F., Physical chemistry of vital phenomena. For students and investigators in the biological and medical sciences. 8vo. pp. vi+240. *figs.* 30. Princeton Univ. Press. 1917.

cells, but with their decomposition products and the exchange between the cell and its surroundings," and that from our knowledge of these "we may speculate on the composition of the cell and the changes that go on in it during functional activity," represents two lines along which productive work is being done and will continue to be done, he is leaving in the background a third line which has also proved helpful and promises still more for the future.

We might wish that the author had given more recognition to the fact that many plant processes are conditioned by the permeability or impermeability of non-living plant membranes. These, however, are very minor criticisms on a book which commends itself strongly by its many excellent features. Among the important topics discussed in the introduction are viscosity as a factor in diffusion, surface phenomena, and the relation of semipermeability to electric phenomena.

His discussion of the plasma membrane (p. 94) as a separate phase which may change with the physiological condition of the cell, and of the protoplasm as sometimes consisting of as many as four phases, in all of which partition solubility must be considered, as well as the molecular condition of each solute in each phase and in the bathing medium, leads him to the conclusion that "all of these factors make the subject of cell permeability a very complex one, no general rules without exception having been found. All we can do at present is to collect data on the permeability of cells to various substances." It is to be hoped that this will commend itself so strongly to biologists that we shall have a larger output of data and a smaller output of theories.

The following shortened chapter headings will suggest the general scope of the book: electrolytic dissociation; osmotic pressure; hydrogen and hydroxyl ion concentration; surface tension and absorption; electrolytes, non-electrolytes, and colloids; enzyme action; permeability and its changes; negative osmosis; anesthesia and narcosis; amoeboid motion, cell division and parthenogenesis; muscular contraction; blood and other cell media.

The "chemical summary" in the appendix will be very useful. The literature list includes over 1500 papers arranged alphabetically according to authors. References in the text to this list facilitate more detailed study of any desired topic. Instead of the conventional index to the text, there is an index to this literature list.—GEORGE B. RIGG.

NOTES FOR STUDENTS

Taxonomic notes.—BLAKE[2] has described a new *Rudbeckia* (*R. Deamii*) from Indiana, closely allied to *R. speciosa*.

COKER[3] has published a detailed and handsomely illustrated monograph of the *Amanita* group as represented in the eastern part of the United States.

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[2] BLAKE, S. F., A new *Rudbeckia* from Indiana. Rhodora **19**:113–115. 1917.

[3] COKER, W. C., The Amanitas of the eastern United States. Jour. Elisha Mitchell Sci. Soc. **33**:1–88. *pls. 69*. 1917.

He recognizes 7 species in *Amanitopsis*, although he regards the genus as "artificial and without systematic significance," separated from *Amanita* by the absence of a single character. In *Amanita*, 27 species are described, with full discussion and citation of stations; among them there are 2 new species and 2 new varieties. The numerous plates are unusually good reproductions of fine photographs.

GARDNER,[4] in a first paper on new marine algae from the Pacific Coast, describes, in collaboration with SETCHELL, 9 new species in as many genera. *Coriophyllum* and *Cumagloia* are described as new genera.

KAUFFMAN[5] has described a new species in *Russula* (*R. ochroleucoides*) and in *Stropharia* (*S. caesiospora*) from Tennessee. They are described in connection with a list of fungi collected in Kentucky and Tennessee during September 1916.

MACBRIDE,[6] in a revision of the North American species of *Amsinckia*, recognizes 23 species, 6 of which are described as new. In further notes on the Boraginaceae, he publishes new species in *Cordia*, *Onosmodium*, and *Lithospermum*, a new variety of *Macromeria exserta*, and new combinations in several genera. In notes on the Hydrophyllaceae, the same author describes a new genus (*Turricula*) founded on *Nama Parryi* Gray, also new species in *Phacelia* (6) and *Miltitzia*, 9 new varieties, and numerous new combinations. A new species is also published in *Petalostemum*, and *Gilia virgata* and its allies (a group of 5 species) are discussed. In cooperation with PAYSON, the same author describes new species in *Arabis*, *Dodecatheon*, *Mertensia*, *Veronica*, *Castilleja* (2), and *Hieracium*, all from Idaho; and also revises series MULTIFIDI of *Erigeron*, recognizing 3 species and 7 varieties, 3 of the varieties being new.

STANDLEY,[7] in a monograph of the Mexican and Central American forms of *Ficus*, recognizes 41 species, 17 of which are described as new.

WERNHAM,[8] in continuing his studies of the Rubiaceae of the American tropics, has described *Neobertiera* and *Blandibractea* as new genera. He also presents the genus *Sipanea*, recognizing 10 species and describing 6 of them as new; also 3 new species of *Cephalanthus* are described.—J. M. C.

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[4] GARDNER, N. L., New Pacific Coast marine algae. I. Univ. Cal. Publ. Bot. **6**:377–416. *pls. 31–35.* 1917.

[5] KAUFFMAN, C. H., Tennessee and Kentucky fungi. Mycologia **9**:159–166. 1917.

[6] MACBRIDE, J. FRANCIS, Contrib. Gray Herb. New Series, no. 49. pp. 79. 1917.

[7] STANDLEY, PAUL C., The Mexican and Central American species of *Ficus*. Contrib. U.S. Nat. Herb. **20**:1–35. 1917.

[8] WERNHAM, H. F., Tropical American Rubiaceae. VIII. Jour. Botany **55**:169–177. 1917.

VOLUME LXIV NUMBER 6

THE
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DECEMBER 1917

RESIN SECRETION IN BALSAMORRHIZA SAGITTATA

ERNEST CARROLL FAUST

(WITH PLATES XXVIII–XXXI AND TWO FIGURES)

Introduction

This problem was undertaken to determine the origin of the secretory tissues and the cause of resin secretion in *Balsamorrhiza sagittata*. The problem was suggested by Professor JOSEPH E. KIRKWOOD, of the State University of Montana, to whom the writer desires to express hearty thanks for valuable suggestions during the progress of the study.

Among the earliest students of secretory organs and their function was MEYEN (13), who stated that "these secretion organs arise from enlarged intercellular passages. One cannot consider them as mere containers, in which the secretion is laid by, but one must compare the containers with their contents to inner glands, and the surrounding walls as specialized glands." This writer proposed that the excretory cells surrounding the secretory canals prepare the balsam and then secrete it through the wall into the intercellular lumen. That the process is surrounded by a sort of mystic vagueness for MEYEN is evident from the description "wonderful" which he applied to the process. In his work on the pine MEYEN (14) found resin not only within the secretory passages and the surrounding cells but throughout the entire stem.

The opinions of the earliest investigators on resin formation were extremely diversified. KARSTEN, WIGAND, WIESNER, and

others of their school considered resin as a destructive slime formation secreted by the cellulose wall lining the cavity, or else a starch derivative. KARSTEN (8) was assured of the intimate relation between the wall and resin gum in the wall, because of the obscurity of the cells in ordinary mounts, whereas the walls became extremely clear when treated with alcohol or ether (p. 317). WIGAND (26) considered resins to be entirely out of the category of secretions, for "a secretion in our sense is only conceivable as a homogeneous material permeable to the cell wall." WIESNER (24) believed the resin masses to be a complex of resin, cellulose, granulose, tannic acid, and "carbonated alkalies," with the cellulose and granulose as intermediate products.

MUELLER (15) and VAN TIEGHEM (22) were unable to find resin in the secretory passages, believing them to be only intercellular spaces. MUELLER was probably the first to use alkannin tincture on dried tissues to test for resin (p. 390). MAYR (12) thought that resin might be secreted by the cells during rapid growth.

Undoubtedly the most careful and authoritative contemporary investigator of resin and the problem of its secretion is TSCHIRCH (21), who has given us a summation of the physiologico-chemical literature of the problem, and in addition valuable evidence contributed from his own studies. TSCHIRCH's investigations have convinced him that resins and ethereal oils cannot diffuse through membranes which are water-permeable or water-absorbent. All such secretions, he asserts, remain where they were first laid down.

Ecological aspects

B. sagittata was first described by NUTTALL (16) in 1841. The plant is a very conspicuous feature of the landscape of the prairies and south hill slopes of Wyoming, western Montana, and British Columbia. Its leaves are large, auriculate, densely hairy, growing up from the permanent rootstock in April at 3500 ft. level in western Montana. The flower stocks are plentiful. The flowers are golden yellow with conspicuous heads. They begin to bloom about the middle of May and continue until July, although they reach their maximum bloom during June.. Very soon after fertilization the flower parts wither, and by the time the seeds are mature in

late July the flower stocks and heads are brown and dry. The leaves remain green until the first heavy frost, when they soon assume a crackling dryness. The plant is a xerophyte, and is commonly found on the flats and upland plains, being especially abundant on the exposed south slopes of the hills. The writer has observed it frequently as high as 6000 ft. and occasionally in the subalpine areas of a still higher altitude.

Specimens of primary rootstock of graduated diameters were dug and dry cleaned and then weighed. They were re-weighed until constant air dry values had been secured. Tables I and II show the results.

TABLE I

SHOWING WATER CONTENT OF PRIMARY ROOTS COLLECTED JULY 1915; COLLECTION DESIGNATED SERIES I

Specimen	1	2	3	4	5	6
Diameter in mm	2.5	4.0	6.0	11.5	13.0	22.0
Weight in gm	0.221	1.429	1.250	2.873	4.195	6.120
Air dry weight	0.088	0.648	0.585	1.505	2.079	3.002
Percentage loss	60.69	54.65	51.45	47.60	50.44	50.95

Average loss of series, 52.63 per cent.

TABLE II

SHOWING WATER CONTENT OF PRIMARY ROOTS COLLECTED OCTOBER 1915; COLLECTION DESIGNATED SERIES II

Specimen	1	2	3	4	5
Diameter in mm	6.0	8.0	9.0	12.0	15.0
Weight in gm	2.337	2.762	3.444	4.144	6.425
Air dry weight	1.107	1.310	1.505	2.038	3.177
Percentage loss	52.60	52.60	56.30	50.80	55.70

Average loss of series, 53.60 per cent.

Tables I and II show a more uniform correspondence for water content in October than in July, although the average water content is practically the same in both series. In general one may conclude that the size of the root has no definite relation to its water content. Within the slight fluctuation the water content is directly proportional to the weight of the root. Also, the average water content is the same at these different seasons of the year.

In direct contrast to these data is the record for water content in random soil samples taken from field areas where *B. sagittata* was growing in abundance. Table III shows such sample records, with normal and air dry weights.

TABLE III

SHOWING PERCENTAGE OF WATER IN RANDOM SAMPLES OF SOIL IN WHICH *B. sagittata* GROWS

Sample	1	2	3	4	5
Weight in gm.....	94.00	126.42	89.27	104.26	110.02
Air dry weight.....	79.11	103.64	77.55	99.12	90.03
Percentage loss.....	15.85	18.02	15.37	4.89	18.18

Average loss of series, 14.46 per cent.

Table III shows a fluctuation of water content in the soil entirely incommensurate with the constant water values of the rootstocks. This may be accounted for in part by the size of the soil particles, since they, too, are far from uniform, and such differences would cause both a difference in weight of soil per unit mass and a consequent difference in capillarity. The fact remains, however, that the plant, irrespective of its root size, selects a relatively constant amount of water from soils that differ noticeably in water content.

Calculations were made also to determine the percentage of resin in air dry roots and leaves. The parts selected were first weighed, then placed in pure ether in an air-tight compartment. They were left in this container for a week, during which time they were shaken frequently. This method of extraction was used after it had been ascertained that ether was the best solvent for the resin of this plant. At the end of this time the ether extract was poured off, filtered, and the ether allowed to evaporate at 20° C. until a constant weight had been secured. For roots dug in July the percentage of pure resin amounted to 3.3; for roots dug in October the percentage was 3.3; for roots dug in May, some three or four weeks after the new growth had begun, the percentage was 5.2. This shows a constant resin value during the resting period and an increased resin content for the growing period. The percentage of resin found in the leaves was 9.8. This value was found for leaves

selected and dried in the middle of May, the time of maximum growth. This resin value was found after the ethereal oil had evaporated. By the osmic acid test it was found to contain no fatty oils. An analysis of *B. terebinthacea* made by Miss HERMA T. KELLEY (**19**) indicated 9.76 per cent resin, 8.96 per cent of which was removed by chloroform and 0.80 per cent by alcohol. In addition to this there were 5.70 per cent oils, 0.42 per cent volatile oils, and 5.28 per cent of fixed oils. LLOYD (**11**) has calculated the percentage of resin for *Parthenium argentatum*, the guayule of the Mexican desert. His values are as follows:

	Per cent resin
Stump	2.46
Wood growth of 1907	1.36
Cortex of above wood	4.06
Growth of 1908	7.56
New growth of 1909 with leaves	2.70
Roots	10.80

These values were obtained from irrigated plants. WHITTELSEY (**25**) secured from 10 to 17 per cent of resin for the field plants of the same species. If the field records are taken, it is evident that by weight the resin content of *B. sagittata* is smaller than that of the related species, *B. terebinthacea*, or of *Parthenium argentatum*.

Associated with *B. sagittata* in a parasitic way is a certain fly of the Typetenid group of the family Muscidae. A complete description of this fly will appear in a separate paper now in preparation by the author. The fly is found in the receptacle of the maturing flower head, living there during the grub and pupal stages of its development. The grub is about 1.8 mm. in length by 0.15 mm. diameter, while the pupa averages 1.5 by 0.15 mm. Usually there is only one individual to the receptacle, but certain receptacles have been observed by the writer in which 5 or 6 of the parasites lived. The grub is very insidious, ordinarily boring a labyrinthine course through the upper parts of the receptacle and into the bases of the maturing seeds. The result is a twofold injury to the seed: an actual destruction of the maturing seed and a stunting of growth in the seed by intercepting the course of nutrition in the receptacle.

Two other important parasites on *B. sagittata* are a nematode and an acarinid. The former is found in the young stem bud before it appears above the ground. The worm eats its way through the bud, mostly in epidermal and cortical tissues, leaving a dry decay behind. Undoubtedly this does much to sap the vitality of the developing vegetative parts, if not entirely forestalling growth. The mite is found in the sinuses between the leaves, sucking out the juices at the bases of the new leaves. Several hundred were found at times in a single leaf bud. This parasite, too, undoubtedly causes serious damage to the plant and serves to control its abundance.

Collection and preservation of material

The material on which this study is based was collected from July to November 1915 and from April to June 1916. Certain roots, stems, and leaf buds were examined fresh, just after collection. Freehand sections were made and observations taken from water mounts. Other material was allowed to dry and was examined as such. However, the greatest part of the material was fixed in various fluids and preserved in alcohol for more detailed examination. Of this last group, material fixed in acid alcohol and preserved in 70 per cent alcohol gave the most satisfactory results. Certain seedlings germinated in the laboratory, illustrating ontogenetic growth, were fixed in Carnoy's fluid. In addition to freehand sections of the alcoholic material, sections of typical roots were made 12 μ thick in series and similar series of the stem and peduncle 8 μ thick. Sections of seedlings were cut 8 μ thick.

Various stains were tried, but the most satisfactory combination was acid fuchsin with malachite green counterstain. This combination gave an excellent contrast, since the lignified hadrome and sclerome elements, as well as suberized walls of the Casparian strip, took on a copper green against the fuchsin background. The ordinary resin stains, cupric acetate and alkannin tincture, were made use of throughout the study. The alkannin was found extremely satisfactory, since it was both specific and rapid. Osmic acid fumes (osmic anhydride) were used to test for fats. Iodine in potassium iodide was employed for starch testing. Chloriodide of zinc was

used to determine the character of the Casparian strip. Slow alcoholic penetration into inulin-testing areas caused a precipitate of this polysaccharide in the shape of sphero-crystals and rhombospheres, while a more rapid penetration caused the material to be precipitated in granular and amorphous masses. Resene was tested for *in situ* by the Mach and Salkowsky-Hesse cholesterol methods (somewhat modified to suit the immediate needs). Crystals of resene found in certain cells were positive to these tests. Similar crystals were found as a check in steam-distilled resene, dissolved in alcohol, and allowed to crystallize as the alcohol evaporated. A more complete discussion of these tests will be found under tests for resene.

The probability of error in resin tests is due in general not to a lack of a specific reagent, but to errors in location of the substance. Due to its solubility in high grades of alcohol it is not impossible that it might become translocated by alcoholic diffusion. Due to its viscous nature it might readily be dislocated in cutting sections from fresh or alcoholic material. The data of certain investigators, among whom are MUELLER (**15**) and VAN TIEGHEM (**22**), show no resin in the resin canals, while SANIO (**18**) and TSCHIRCH (**21**) were unable to find the secretion outside of the canals. Errors in technique must have been responsible for this. TSCHIRCH considered ordinary methods of technique inadequate for the elimination of the error and made use of a method adapted from MUELLER (*loc. cit.* p. 390). He dried the material at 100° C. for some time before cutting. He then stained with alkannin tincture in water (*2* parts of the tincture and 5 parts of water). The former procedure allowed all volatile oils to be driven off and hardened the resin to a tough gummy consistency, so that it was not easily removed from its original position by the section cutter. The latter diluted the tincture so that the resin would not readily dissolve in the alcohol. By this method TSCHIRCH was able to demonstrate resin in the form of a dense slime in the canals of *Imperatoria Ostruthium*, *Arnica montana*, and in the leaves of *Abies pectinata* and *A. Normanni;* while the surrounding tissue, especially the secretory cells, was free from resin content. The writer has given due weight to this possible source of error, and has made many preparations from

live material, alcoholic, and dried preparations. It is only by a study of all these preparations that he feels able to present authoritative data.

Germination tests

The seeds of *B. sagittata* are ripe about the first week of July. From that time they soon become dislodged from the receptacle and fall to the ground. Between July 6 and July 15, 1915, several thousand seeds were collected and sorted into two tentative groups, those considered viable and those considered non-viable. The latter group comprised about 90 per cent of the whole. Of this non-viable group almost half were eaten at the base of the seed by the Typetenid parasite, and the remainder were small and shriveled, due to lack of nourishment. This non-viable group was discarded. Of the seeds saved, 100 choice ones were selected October 19, 1915, and weighed. Their total net weight was 1.041 gm. They were then soaked in concentrated sulphuric acid for 8 minutes, carefully rinsed in distilled water several times, and placed in a sterile moist chamber at about 30° C. during the test. The record is as follows:

SERIES I

October 19; 100 selected seeds weighed, sterilized, and set to germinate in sterile moist chamber.

November 3; one seed beginning to burst testa; hypocotyl protruding.

November 5; 3 seeds burst testa; hypocotyl of one 11 mm. long.

November 6; 13 seeds found soft and decaying; thrown out.

November 10; 11 seeds found soft and discarded.

November 11; 5 seeds germinating; 4 thrown off testa.

November 12; 12 seeds found soft and thrown out.

November 14; 8 seeds germinating.

November 17; mold developing; those seeds not yet germinating but considered sound rinsed in weak formalin solution, then thoroughly rinsed in distilled water.

November 28; 10 seeds germinating; 5 of these fixed in Carnoy's fluid, 5 transferred to cork supports in beakers of water and allowed to continue growth; all ungerminated seeds discarded.

Later, no further growth.

SERIES II

November 18; 100 seeds selected, soaked in sulphuric acid for 5 minutes, thoroughly rinsed, and set to germinate between damp filter paper in chamber as in Series I; average temperature 30° C.

November 28; mold developing; seeds rinsed in formalin solution, rinsed in distilled water, and returned to damp chamber.

December 1; culture found dry; had been dry about two hours.

No germination in this series.

SERIES III

January 25; 100 seeds selected, soaked in sulphuric acid, thoroughly rinsed in distilled water, then placed in sterile moist chamber between filter paper; distilled water supplied as needed drop by drop by siphon apparatus; temperature 25° C.

January 31; first seed bursts testa; no mold.
February 1; 5 seeds found soft and discarded.
February 10; 3 seeds germinating.
February 18; 4 seeds germinating.
February 24; 6 seeds germinating; no mold.
February 29; 8 seeds germinating; several of the remainder soft, discarded.
March 4; seeds dry for several hours; no subsequent germination.

An examination of these records shows certain interesting and significant points. A comparatively small percentage of seedlings germinated from selected seeds, due to lack of viability in apparently viable seeds and to infection during the germination tests. An extremely small percentage of seeds germinated from the total seed production. Series I gave a total of 10 per cent of seeds germinated from 100 selected seeds. Series II gave no germination, due to desiccation antecedent to expected germination. Series III gave an 8 per cent germination within the same time limit as Series I (less one day), but at a lower average temperature. The average for Series I and III is 9 per cent. A more elaborate and critical study of the germination values for *Parthenium argentatum* by KIRKWOOD (**9**, p. 39) gave 10.8 per cent for selected seeds of that species.

Since the selected seeds comprised only about one-tenth of the total seeds produced, an average of less than 1 per cent (0.9) is obtained for the ratio of seeds germinated to the total of seeds produced. Although the plant is a perennial, the severity of the winters in the exposed places where the plant grows kills out many of the rootstocks. Taking into consideration the infection of the bud and the stem by nematodes and mites, an enormous seed production would seem necessary to maintain the plant as the dominant member of the society in which it grows.

A survey of field plants was made during May 1916. Plots covering areas 300 ft. square were studied, and the number of root-stocks counted and the seedlings in those areas listed. For two such plots about 800 plants were found, equally divided between the two plots. This number comprised all plants of *B. sagittata* of all sizes and ages within the plots. An accurate idea of the distribution of the plants is seen in text fig. 1. Areas 4 ft. in radius were

FIG. 1.—Field of *Balsamorrhiza sagittata* in vicinity of Missoula, Montana, in May 1916.

closely inspected around each plant, the plants receiving numbers as the listing progressed. In plot 1, in the count of the first 100 plants, one seedling each was found for numbers 2, 3, 4, 8, and 100, no other plant having the seedling within this radius. In plot 2, for the first 100 plants counted, numbers 11, 49, 69, and 70 had one seedling each, while number 68 had two. In a second 100 in plot 2, numbers 41, 61, and 91 had one seedling each. Of those plants observed about half had borne seeds the previous year, or

about 200 per plot of 300 square ft. had been seed producers. Yet only 5 seedlings were found in the count in plot 1, only 6 in the first count in plot 2, and only 3 in the second count in plot 2, averaging 4.66 per cent, a much lower average secured than for seeds germinated indoors. It is evident from the dominance of this species in the society in which it lives that it depends largely upon the continued growth from the rootstock from year to year for maintenance of its dominance. It is not unusual for the individual rootstock to produce 100–300 seeds. This would more than replace the plant each year if the laboratory germination test were effective in the field, but the lower germination record for field plants indicated beyond a doubt that the plant could not be replaced each year by the new seedlings.

The germination in the field is comparatively late. The first of the consocies to germinate is the seed of *Lupinus ornatus*, which begins about March 1. Since *B. sagittata* does not fruit until the third or fourth year, but gives up all the time and energy the first two years to growth and food storage, it is evident that early germination is not essential to the best interests of the plant; yet the blooming rootstocks of *B. sagitatta* are in flower long before the lupine.

Of the factors determining germination, air (oxygen) is undoubtedly the most important. A test of this factor was made in a group of seeds not included in the series just cited. The same conditions prevailed in this series as in the recorded series, except that they were covered with a sterile crystallizing dish so as to exclude air. There was no germination. A careful comparison with the recorded series seems to indicate that oxygen is more necessary to prevent fungous growth than as a factor in the metabolic processes of germination per se. When seeds are once set to germinate, moisture is constantly necessary for germination, as indicated in Series II and III.

The temperature coefficient of germination is interesting. It is evident that germination is more rapid at first at 30° than at a lower temperature. However, although germination at 25° is slower, that appears to be a more advantageous condition, since at that point a maximum growth of the plant is effected for a

minimum growth of fungus. Undoubtedly under field conditions the temperature is constantly less than 25° C., except for a short time during the warm afternoons. In fact, practically any night during the germination period (middle of April to middle of May) a freezing temperature may be recorded.

Certain seeds which actually germinated or commenced to germinate had been injured in the region of the root cap or even in the region of the meristem of the root. This was the cause of a decreased vitality in the entire plant and was often the occasion for rapid bacterial infection. This injury was originally due to the Typetenid parasite in the receptacle of the flower head. Such an injury must be a source of constant decay to germinating seeds in wet ground.

Structure

ROOT.—In the developing seedling of *B. sagittata* at a very early stage, a day or so after the seedling begins to break through the testa, certain cells begin to differentiate into protoxylem. These occur at four angles of the root section, forming a tetragon, giving rise to the tetrarch structure of the primary root. At first these spiral tubes develop singly, but may later be followed by one or two others centripetally at each angle of the tetragon (fig. 7). As might be expected from their later origin, these secondary spiral vessels are somewhat larger than the elementary vessels. At this earliest differentiation of protoxylem there are no indications of protophloem from procambium. Very soon, however, such differentiation begins midway and slightly centrifugal to the line joining the first quartet of protoxylem elements (fig. 8). The procambium cells in this region divide tangentially, with apparent irregularity, developing protophloem externally and at the same time intermediate protoxylem internally. Such growth is represented in figs. 9 and 10. These periclinal divisions continue until 4 or 5 concentric rows of phloem are formed and until the xylem almost completely envelops the axial plate. At this time the axial plate is still composed of undifferentiated tissue quite irregular in contour, strikingly similar to the stem pith of the plant. The leptome strands are limited externally by the undulating endodermis, con-

spicuous now (fig. 10) by anticlinal suberization. The appearance of the thickenings is knotlike or looplike along the radial walls. The endodermis, unlike that of *Parthenium argentatum*, contains no starch grains such as commonly occur in higher plants.

The secondary xylem contains not only well defined spiral vessels and tracheids, but vessels of intermediate type. For instance, in fig. 11, *c* and *d* with bifurcating spiral reinforcements are not far removed from *a*, the true spiral type, while *e* more nearly approaches the eyelet type so characteristic of the tracheids.

In the dicotyledons the usual type of axial structure is parenchymatous; but such is not the case in *B. sagittata*, for there the wood elements soon work centripetally, crowding against the original plate cells. The latter become sclerified, so that the plate becomes a solid disk of vessels and sclerome. Such sclerification begins before radial suberization of the endodermis and considerably earlier than resin duct formation. The centripetal crowding with the addition of the new xylem elements increases the actual size of the region within the cambial ring.

The suberized endodermis serves a twofold purpose. The suberization thickens the walls and allows the endodermis to act as a supporting girdle, and, in addition, acts as an impervious barrier against an external translocation of food material. Russow (**17**) has described two types of suberization of endodermis, that in which the radial and one tangential walls are thickened (his "C" type), and that in which the entire wall is thickened on all sides (his "O" type). Haberlandt (**6**, p. 372) suggests that such distinction is not of great mechanical importance, since variations may occur within the same genus, such as *Carex*, *Smilax*, etc. Although the "C" type is the most usual in *B. sagittata*, there also occurs the "O" type, and in woody secondary roots a thickening which may be designated as an "H" type (fig. 12). In the primary root of 5 mm. or over, the suberized endodermis is interrupted in regions between resin canals by phloem strands which cross into the cortex in these regions, leaving open an avenue for translocation of materials in these special places (fig. 13, *ph*). The origin and development of the resin canals will be discussed later in this paper.

In the older rootstocks of two or more years' growth three regions may be distinguished, a basal primary root, a median swollen region, and two or more branched root growths above the swelling. From the upper reaches of these proximal root branches arise the aerial portions of the plant system. The lowest root region is characterized by a single row of resin canals and an axial stele, while both of the other parts have two concentric rows of resin canals (fig. 14). Cross rays connect these longitudinal canals at frequent intervals. These old rootstocks are further characterized by lysigenous splitting of the now functionless rays, so that the wood is split apart in almost every ray region (fig. 15, l_1, l_2). This cracking is probably caused by tension in the wood areas and a shrinking of the cells in the near vicinity.

The subsidiary root system of *B. sagittata* varies from the main system in that it is diarch in type. The protoxylem first becomes differentiated as two groups at opposite poles, with evidence of protophloem developing intermediately (fig. 16). By the time the suberization of the endodermis occurs, intermediate wood elements have developed and the axial plate is well sclerified (fig. 17). It is not until considerably later that the resin ducts arise (fig. 18).

The root of the plant has a rather large wood area compared with the extra-cambial portion of the root. Table IV shows that it is practically a ratio of two to one through all stages of secondary thickening.

TABLE IV

Number	Diameter of root	Ratio
1	2 mm.	2:1
2	3.5	2:1
3	4.5	2:1
4	12	8:5
5	12	2:1

This excess of wood tissue may be accounted for by the area occupied by the rays extending between the wood elements. In no. 5, with two rows of resin canals, lysigenous cracks in the ray region occupy about half of the wood area.

While the tracheids conform to the usual type for Compositae and the phloem cells show no unusual 'characteristics, certain

features of the stone cells deserve special consideration. These cells are found principally in the hypodermal region and give a hardness to the cortex, which makes untreated material difficult to section. They take on a vivid green with the malachite stain. They are somewhat larger than the surrounding cortical parenchyma, due to their thickenings. In surface view they present a polygonal appearance, with bluntly rounded corners (fig. 19, *a–d*). A view at the edge of the cell shows circular pores which enlarge and approach one another as they invade the center of the cell. The center of the cell is an irregular space devoid of the sclerified material, usually filled with ordinary parenchyma cell protoplasm. This content fails to react to starch, oil, or resin tests. As the canals of the cells near the lumen, they anastomose in pairs or triplets, giving an appearance as shown in fig. 19, *d*. The cells have at least one transverse diameter longer than the longitudinal (compare fig. 19, *c* with *d*). This same type of stone cells also occurs in the axial plate of old woody roots (both primary and secondary), and in the wood of subsequent formation, although it is never found in phloem regions. In the latter tissues it is supplanted by bast strands (fig. 13). The stone cells usually occur in groups of five or six.

STEM AND PEDUNCLE.—The hypocotyledonary stem contains the tetrarch arrangement, as shown in fig. 20. The phloem is exarch and the xylem endarch, with protoxylem innermost. As progress is made up the stem, the meristematic region where the bud resides is approached, containing secondary stem, leaf, and flower structure. At this place the four main strands each give off two anastomosing bundle strands to the bud, while the major portion of the bundle strands continues into the cotyledonary collar (fig. 21). Slightly above the section diagrammed in this figure certain changes occur in the bundle strands. These are best illustrated by a comparison of the section shown in fig. 22 with fig. 24, a diagram of the course of the bundles, seen longitudinally. Between levels *cc* and *dd* strands are given off from *w* and *x*, which unite above *dd* to form a median strand *p*. Coincidentally laterals from *y* and *z* form the median strand *s*. Similarly above the section *dd*, *x* and *y*, *z* and *w*, give off subsidiary strands which anastomose in pairs to form respectively

r and *t*. A section taken between *cc* and *dd* might show all the way from 4 to 12 strands, depending entirely upon the exact level of the section, and a section taken above *dd* might show from 6 to 8 for the same reason. Slight variations in the origin of coincident laterals due to unequal nourishment would be shown in an odd number of traces. Returning to figs. 20–23, diagram 22 occurs about the level *dd*. Laterals from *w* and *x* have been given off to form *p*, but have not yet anastomosed. A lateral from *z* to form *s* has been separated from the parent bundle, but its mate from *y* is still intact within *y*. Meanwhile traces from *x* and *z* have already arisen for the formation of *r* and *t*, although their mates are still within the main bundles *w* and *y*. Hence the actual derivations are atypical in location, although the end results are the same, that is, 4 median strands (*p*, *r*, *s*, *t*) derived from uniting limbs of the 4 original bundles (*w*, *x*, *y*, *z*). The section in fig. 23 shows a level above *dd*, where laterals are being derived from *t* and *w*, *y* and *s*, *y* and *r*, to form strands of tertiary rank, with laterals from *w* and *p* not yet derived. Already *x* and *z* have been broken up by a twofold bifurcation.

Certain atypical traces were found in the study of the tissues of *B. sagittata* at this period in its development. In one series of sections the laterals from *x* and *p* received a trace from below. Further observation showed this trace to end blindly at a lower level. In another series the lateral from *z* to *s* was found to give back certain strands to *z* before the lateral united with its mate from *y*. In such cases transverse sections alone would be difficult to use in tracing such bundle anatomy. In older stems and in the peduncle 8–24 traces are derived, dependent on the amount of conduction required in these parts.

LEAF.—The leaf type of a seedling is defined with reference to the number of traces in the blade which appear as separate entities at the origin of the leaf blade from the petiole. In his studies on some 50 seedlings of representative groups of Compositae LEE (10) has chosen *Silphium perfoliatum* as the type for Heliantheae, to which tribe *B. sagittata* belongs. The general superficial appearance of *S. perfoliatum* and the plant under consideration is very similar. Both seedlings are large and hardy, with no secondary

roots up to this period of development. In writing about the bundle strands of this type LEE states as follows:

> As usual in this order the single vascular bundle at the apex of the cotyledon first divides into 3, after which, in correspondence with the large size of the cotyledons, each main strand gives off a large number of smaller bundles. At a lower level, these begin to re-fuse with the larger strands, and at the base of each cotyledon only 5 vascular strands remain, a large median one and two smaller laterals on either side. In the pronounced cotyledonary tube the extreme lateral and smallest bundles fuse with the corresponding bundles from the other cotyledon, and the composite structure produced, after decreasing in size, moves around and joins on to one of the remaining strands. At a still lower level in the cotyledonary tube, the remaining lateral bundles fuse in pairs, so that 4 canal vascular strands enter the hypocotyl.

Upon examination of seedlings of *B. sagittata* it is evident that neither the cotyledons (figs. 22–24) nor the first true leaf (fig. 6) possess bundle traces exactly corresponding to the type for the Heliantheae. There are considerably more than 5 strands for the region above the origin of the blade (fig. 23), but at a level just below the cotyledons in the cotyledonary collar (fig. 24, level *dd*) only 6 strands are found, although in certain sections even below this level (fig. 22) a greater number is indicated, due to peculiarities of transverse anastomoses. Even the true leaf (fig. 6) shows only 3 bundle strands at the origin of the blade from the petiole. It may be said, therefore, that for *B. sagittata* we have a type of bundle anatomy of somewhat fewer strands than for *Silphium perfoliatum*. With these exceptions it has a general resemblance to the tetrarch anatomy of the Heliantheae.

RESINIFEROUS DUCTS.—A root of a young seedling with cotyledons not yet outspread shows clearly the resin secretion from the protoxylem outward through the cortex. There are large drops of resin at the time the endodermis begins to take on suberized thickenings, yet at this stage no resin ducts have formed. Not until the seedling is some 60 days old do the ducts begin to form in the root. The development, although surely determined beforehand, does not occur until after resin formation. The method of development is schizogenous. First a periclinal division occurs in the endodermal cell opposite a group of tracheids. This is followed by an anticlinal division, so that 4 cells arise from the original endodermal cell

(fig. 26). A lumen develops in the midst of the 4 cells, which canal becomes the cavity for resin secretion. Usually the 4 cells now divide obliquely with new planes of division parallel to the walls of the duct, so that the duct becomes lined with 2 layers of cells (figs. 27, 28). A consequent cleavage at right angles to the walls of the duct gives rise to 8 cells immediately lining the duct (figs. 29, 30). This ring of ducts in the cortex, just outside the endodermis, is the usual complement of ducts for the root. As the root grows, however, room is made between the older ducts and new ones are formed. The resin ducts of the root are continuous from the basal region to the junction of the root with the stem. These ducts are somewhat more undulatory than are the tracheids. At times there is evidence of the fusion of 2 ducts, but this is merely due to a breaking down of internal processes from the cells surrounding the lumen rather than an anastomosis.

An examination of seedlings of 2 mm. or over shows in the hypocotyl 2 concentric series of resin canals, the outer series continuous down through the entire root system, and the inner merely potential in the younger seedlings. The 2 series are connected by radial canals between the longitudinal lumina of the series and by transverse canals between consecutive longitudinal canals of the same ring (fig. 31). Moreover, the inner series is capable of ventral extension in roots of one year or over, so that they extend down and around the median enlargement of the root. At this place they all anastomose in a common center (fig. 14).

This type of concentric rings with radial anastomoses corresponds to observations made by CALVERT and BOODLE (2) for *Manihot Glaziovii*, but is the reverse of LLOYD'S (11) observations on *Parthenium argentatum*.

The ducts in the stem consist of 2 separate systems. These systems have similar origin and structure, but different location. One series is found in the pith opposite the wood of the bundles, while the other series occurs in the cortex opposite the interfascicular region, almost within the interstices between the phloem of the bundles (fig. 25). These ducts arise somewhat earlier than those of the root and apparently are not connected with those of the root system in any way. They are continuous throughout the

entire stem, although they are intercepted in certain regions by processes from the lining cells, as shown in fig. 35. The origin of both these systems in the stem is schizogenous and follows the same sequence of development as outlined for the duct system of the root. HOLM (7), working on the anatomy of *Solidago odora* (pp. 252–254), quotes VAN TIEGHEM as saying that resin ducts have only been observed in the cortex (primary) "in certain species of *Solidago*, including *Kleinia;* otherwise these ducts are frequent in the pith and in the secondary tissues." The two series of ducts in the stem of *B. sagittata* indicate a composite type of duct anatomy, in that they supply a duct system in the primary cortex, hitherto observed only in species of *Solidago*, and in addition supply the usual system of the pith. These ducts, too, are subsequent to resin formation in the stem.

The resin ducts of the leaf are merely upward prolongations of the stem systems, corresponding to the bundle trace relationships already indicated. For each bundle in the leaf there are two canals, one occurring on the upper side of the leaf and the other one on the lower side opposite the hadrome elements. DEBARY (4) gave a very complete table of the duct systems as far as they had been worked out in his day, VILLUEMIN (23) has studied it in certain species, and COL (3) has added to the knowledge of the subject, but a thorough revision of the literature needs to be made in order to bring the knowledge up to date.

Since VAN TIEGHEM prepared his schematic outline for types of resin duct distribution in the stems of Compositae, at least two new types have been observed, namely, the *Solidago* type described by HOLM (7) and the type represented by *B. sagittata*, described in this paper. For this reason it is necessary to reconstruct VAN TIEGHEM's scheme to include the more recent observations.

OUTLINE KEY TO SECRETORY PASSAGES IN STEMS OF COMPOSITAE TYPES

I. Stem containing passages within bundle sheath
  A. Passages confined entirely to medullary region . . . *Ageratum conyzoides*
  B. Passages both within and without bundle strands
    1. Only one medullary passage for each leaf trace bundle
      a) One medullary and one cortical passage

i. Both passages opposite the bundle.....*Solidago limonifolia*
ii. Medullary passage opposite the bundle, but cortical passage in the interstices between bundles ..*Balsamorrhiza sagittata*

b) One medullary and several cortical passages
Serratula centauroides

2. A group of medullary passages for each group of cortical ones
a) Group compact.....*Carduus pycnocephalus*
b) Groups in curved series.....*Helianthus tuberosus*

II. Passages wholly without bundle strands
A. Passages external; not walled in on inner side by endodermis or pericycle.....*Solidago odora*
B. Wall of passages partially formed by endodermis or pericycle
1. Passages single, not in groups
a) One passage in middle of outer margin of each main leaf trace.....*Senecio vulgaris*
b) One passage in middle of outer margin of each main leaf trace; in addition one passage for each single bundle in such united trace.....*Aster* sp.
c) One passage on each side close to phloem of each main bundle trace.....*Tagetes patula*
2. Passages in groups
a) Three to five passages opposite outer margin of phloem and of main bundle.....*Silybum marianum*

Physiology of resin secretion

Numerous theories have been proposed to explain the origin of resin and the methods of resin secretion. Among the more important sources conceived as a basis for resin formation may be named the following: starch, cellulose, tannic acid, phloroglucin, a hypothetical glucoside, terpene, and even chlorophyll. As diversified as are these substances, there may be at least superficial reasons for relating resin to any one of them. However, only a deeper analysis of the problem, following out a particular coincidence of resin and one of these materials, will show whether the relationship is a genetic one or not. Evidence is here presented showing certain relationships of the resin secreted by *B. sagittata*.

The resin of this plant appears as a viscous exudation, especially from newly dug roots. It is a light lemon color in smaller quantities, but in larger amounts (ether extraction) it appears a golden yellow. It contains a small amount of essential oil, but gives no

tests for fatty oils. In the roots of young plants (two years or less) it is found mostly in the outer ring of canals, while in old roots it occurs in the two concentric rings of canals, together with the radial anastomoses.

As has previously been mentioned, the ordinary resin tests are cupric acetate and alkannin tincture. The acetate requires several days and imparts a brilliant emerald to the resin. The alkannin causes the resin to take on a brilliant crimson in a very short time. The resin may be distinguished from oils of a fatty nature by the osmic anhydride test. The alkannin is much more soluble in the higher grades of alcohol, but such a high concentration of the solvent is not desirable, since it also acts as a ready solvent for the resin.

The TSCHIRCH test for resin, modified from MUELLER, was used by TSCHIRCH for demonstrating that resin was present in the lumina of canals of *Imperatorium Ostruthium*, *Arnica montana*, *Abies pectinata*, and *A. Normanni*. In fact, TSCHIRCH noted a layer of slime among all schizogenously formed canals. The writer has made use of this technique for testing resin in *B. sagittata* and *Parthenium argentatum*. These preparations show resin in the canals, as described by TSCHIRCH, but in addition demonstrate resin in the newly formed xylem, an abundance of it in rays and inner regions of cortex, including the cells immediately surrounding the canals, and *great masses of resin in the cambium*. Such dry preparations demonstrate resin in the identical locations as the aqueous mounts from fresh material and alcoholic material. In this wise an accurate check has been secured on the demonstration mounts.

An analysis was then made to discover the approximate relation of resin to other organic materials. Resins are classified according to their reactions to four kinds of tests: resino-tannol, resene, resiniferous oil, and resinic acid tests.

The resino-tannols are those resiniferous materials which react to tannin tests. For example, when ferric chloride is added to a solution of resino-tannol, iron tannate is formed as a precipitate. Other reagents used to test this relationship are potassium bichromate, lead acetate, potassium hydrate in alcoholic solution, and nitric acid. Should any of these reagents give a positive test, an exceedingly difficult problem would then confront the investigator.

Since tannin is not a single compound, but a convenient name for a related group of compounds, separate tests of the entire group would then be necessary. Moreover, as TSCHIRCH has pointed out (*loc. cit.* 1142), such a test would not necessarily prove a genetic relationship, since tannin might be merely a by-product and not its source.

Samples of the resin (ether extraction) from *B. sagittata* were submitted to the resino-tannol tests. All samples gave negative test except the one where nitric acid was used as the reagent, in which case the test was atypical. This test was so positive, however, that it served to indicate a possible relationship of another nature. Two or three drops of the pure resin were placed in concentrated nitric acid. The resin globules became dark brown, with a violent evolution of nitric oxide in the course of two minutes, accompanied by the formation of a cellulose membrane across the top of the solution. When heated, this membrane burned with a warm yellow flame and heavy smoke, leaving a black char. The odor was like that of burning celluloid. The test was then repeated with resin dissolved in 95 per cent alcohol. The reaction was delayed, not taking place for 5 minutes, but was accompanied by a more violent evolution of the gas. When the test was repeated with the resin dissolved in absolute alcohol, the test reaction did not take place for 6 minutes, and was even more violent than on either of the previous occasions. Such a reaction would indicate a relationship to cellulose or other carbohydrate.

The second group of resins are called resenes. They are the ones showing kinship to the terpenes and the fatty aldehydes. The modified cholesterol tests are applied to these substances. Two of the more common and specific ones are the Salkowsky-Hesse and Mach reactions. In the Salkowsky-Hesse test 0.002–0.003 gm. of the resin is placed in 3 cc. of chloroform and shaken with 3 cc. of concentrated sulphuric acid. The chloroform solution is then evaporated in a porcelain dish and the color of the residue noted. The color differs for various known resenes, from orange through lavender to blue, but is always a constant index for a particular resene. Substances that are not resenes do not give such color tests. In the Mach tests 0.003 gm. of the resin is placed in 1 cc.

of concentrated hydrochloric acid and evaporated in a porcelain dish and the residue washed. If the test is positive, the residue is usually blood orange or red. Both the Salkowsky-Hesse and the Mach tests were applied to the July and October resin of the *Balsamorrhiza*. The results were negative.

As previously described, the fatty oil test is made with osmic acid. A slide with a thin smear of the resin is inverted over a solution of the acid or of the crystals. The fumes of the reagent cause fatty substances to blacken. When the osmic anhydride was applied to resin of *B. sagittata*, no positive test was secured, even after prolonged application.

If resin gives an acid reaction to litmus or requires several portions of one-tenth normal sodium hydrate to neutralize, it is said to be a resinic acid. Such acids unite with ammonium hydrate and the hydrates of the alkali metals to form unstable resinic esters. A great number of these resinic acids are known, although their chemical formulae have been worked out only empirically. Certain of these acids have been distinguished by the type of ester formed with ammonium hydrate. For example, the group to which pimar acid belongs builds a very beautiful acid ammonium salt, while the group to which abietic acid belongs forms with ammonium hydrate a non-crystalline gelatinous emulsion (see TSCHIRCH, *loc. cit.* 519). The resin of *B. sagittata* gives a very decided acid test. It combines with ammonium hydrate, potassium hydrate, and sodium hydrate to form resinic esters. Moreover, the ammonium ester is an emulsoid.

The evidence gained from these tests shows that the resin of *B. sagittata* is a member of the resinic acid group, giving an ester with ammonium hydrate similar to that of abietic acid, and that it has certain relationships to carbohydrates in that it forms a nitrocellulose when reacted upon by nitric acid.

It was found that by a distillation of the resinic acid, either from the gross plant structure or from ether extracted resin, in the presence of steam, an entirely new product was formed. The substance had a tendency to crystallize upon cooling below 25°, and gave off a very characteristic pungent odor, sweetish, but very irritating to the mucous membrane. The substance was white, opaque, and

crystallized out of water in a very elaborate form, simulating frost crystals. Later it was found that it crystallized as long monoclines out of alcohol or ether. The two resene tests were applied to this substance, with positive results in both cases.

SALKOWSKY-HESSE TEST

Sulphuric acid solution after shaking: golden yellow.

Chloroform solution before evaporation: pale yellow, nearly colorless.

Residue after evaporation of chloroform in porcelain dish: first, bright yellow; later, rich dark brown; red brown; ending in deep violet.

No fluorescence.

MACH TEST

Color of residue from evaporation of alcoholic solution of resin with hydrochloric acid and ferric chloride: dark red.

This resene is saturated, failing to absorb iodine, but is weakly acid.

These positive tests, together with the general physical properties of the substance, were proof that the material under analysis was a resene, a type of fatty aldehyde. It was further discovered that all of the resinic acid was converted into resene in the process of steam distillation.

Two preparations of resene from steam distillation of spring roots were made during August 1916. One of these was placed in a glass-stoppered bottle and the other in a loosely corked vial. An examination after 6 months showed that the former preparation was in the original crystalline state, while the latter had been converted into a lemon-colored resin, and had completely lost its crystalline structure. This fact supports the view that the resene had been converted into resinic acid by an oxidative process, such as holds true for terpenes in general. This process follows the natural method expected in the plant tissues, and is the reverse of the reduction process in the presence of steam.

The discovery that resene is derived from resinic acid gave rise to the inquiry as to whether resene might not be found in the *Balsamorrhiza* plant; in short, whether there might not be a genetic connection between the two substances in the plant itself. The following methods were carried out in this inquiry: modified resene tests *en bloc* and modified Mach tests applied microchemically.

In the tests *en bloc* equal portions of *Balsamorrhiza* roots (alcoholic preservation of August material) and sprouting stem buds (fresh March material) were each placed in 5 cc. of chloroform and left for two days. The plant tissues were then removed and 5 cc. of sulphuric acid added, according to the Salkowsky-Hesse method, and the mixture thoroughly shaken. The results are given in table V.

TABLE V

	August root	March bud
Sulphuric acid solution	Pale tan	Colorless
Chloroform solution	Colorless	Colorless
Residue from evaporation	Colorless	Lavender to violet
Iridescence	None	Marked between solutions

The Mach test (modified) was used on sections of rapidly growing stem buds, just previously placed in 85 per cent alcohol. Sections of this material were cut in 95 per cent alcohol; 1 cc. of this alcohol, 1 cc. of ferric chloride, and 1 cc. of hydrochloric acid were mixed and the sections transferred to this mixture on a depression slide. The slide was then gently heated until the mixture was reduced to about 1 cc. Even from gross inspection a typical Mach test was produced in the vascular tissues. Examination under low power of the microscope showed reactions in the following places: heavy stain in the cambium and rays (identical with regions testing heavily for resin in fall tissues); specially marked test against walls of endodermis facing cortex; all through cortex and pith to more or less degree. In the heavily testing regions masses of monoclinic crystals were found, deeply impregnated with the stain from surrounding crystals that had dissolved (fig. 37). This same test was applied to roots of the August collection, preserved in 60 per cent alcohol. The results of the test were negative. This very specimen block had been used previously for resin tests and had yielded a decided resin test in the vascular and conductive areas.

These two tests, the Salkowsky-Hesse and Mach, modified to meet the needs of the material under investigation, applied to *Balsamorrhiza* material, showed a negative test for fall roots and

a uniquely strong positive test for the spring bud region. In fact, a comparison of the former test with the present one would indicate a much higher percentage of the resene in the spring bud than was necessary for a test reaction. Moreover, the Mach test both checked up the results obtained in the Salkowsky-Hesse reaction and gave the precise location of the resene in the growing bud.

A final test to check up the previous determinations consisted in placing some of the material of the fall collection and the spring collection in absolute alcohol-ether, half and half, for a period of two days, then allowing the filtered solution to evaporate. No crystals were found from a careful examination of the fall roots, yet an abundance of crystals of the monoclinic type were secured from the spring stem material.

The evidence secured from these reactions for tissues of *B. sagittata* shows (1) that resene is found in the growing plant tissues, in the meristem and conductive areas; (2) that resene is found in the same region in spring tissues where resinic acid is found in the fall tissues; and (3) that resinic acid areas in fall tissues test negatively for resene.

In the middle of May roots dug about May 1 were tested for percentage of ether extract. Such data are recorded in the ecological section of this paper. This material shows both resene and resinic acid present in tissues at this particular time of the year, when the leaves had been well developed and metabolic processes were near the zenith point.

When tests were made on various parts of the plant to discover whether a Mach test could be secured, the test was negative. These tests were made on stem and root tissue and on cotyledons and embryo within the seed coat. Later certain crystals were noted in the connective and storage tissues of the plant, spheroidal in shape, with rays arising from an eccentric umbo. The crystals were observed in material which had been preserved in alcohol *en bloc*. These crystals did not occur in fresh aqueous mounts nor in fresh material sectioned and mounted in alcohol. The type of the crystal was such and its reaction to reagents such as to establish

it as the crystallized inulin, a colloidal polysaccharide. In ordinary growing tissues these crystals are deposited in a viscous lemon-yellow mass, but in alcohol they undergo certain changes in shape. In readily permeable tissues they are laid down as granular masses, but where there is slow alcoholic penetration they are laid down as sphero-crystals. Such crystals are well illustrated and their location shown in fig. 36 (*si*). They are found in connective tissue, especially in the rays and in the inner cortex. In this same specimen the canals are filled with resin. The semiviscous, semigranular resene is well brought out in fig. 16, the section of a very young subsidiary root without secondary thickenings yet developed. In fig. 17, the section of a subsidiary root further developed, is shown in the more permeable outer region of the cortex the semiviscous, semigranular inulin, while the sphero-crystals are found in the inner cortex, not so permeable to alcohol.

Other observations on the growing stem buds showed the following relationships. Young etiolated stem buds showed no inulin, while green stem buds were filled with inulin. Such observations are proof that the result of the photosynthetic process in *B. sagittata* is inulin. Such a substitute for starch is found in the related Compositae, *Helianthus annuus*, *Inula Helenium*, and for roots of *Dahlia* spp.

As the microchemical tests progressed, evidence became stronger that a genetic relationship existed progressively in turn between each two of the three products found in *Balsamorrhiza*, namely, inulin, resene, and resinic acid. The hypothesis built up on this evidence may be stated thus:

Inulin < resene < resinic acid; in other words, inulin, a polysaccharide, formed in the plant in the process of photosynthesis, by a process of polymerization is changed to resene, and by reduction the resene is altered to resinic acid, a waste product of the plant. The direct evidence supporting this view may well be summarized at this point: (1) etiolated stem buds contain neither inulin nor resene, while green leaves test for both coincidentally; (2) resene and resinic acid are found in the stem and root at the same time; resene more frequently occurs in conductive tissue and

resinic acid in ducts and canals; (3) resene is derived from resinic acid in the presence of steam; (4) resene is converted into resinic acid in the presence of oxygen.

A suggestion of the effects of resinic ester and resene on the vegetative growth of *B. sagittata*, and in consequence an idea of the physiological nature of the products, is shown by the effect of these substances on the living protoplasm. Although this plant is not listed among the poisonous plants of the western stock ranges along with the death camas (*Zygadenus venenosus*), the loco weeds (*Aragallus* and *Astragalus* spp.), the larkspurs and the lupine (*Lupinus ornatus*), it is the common belief of stockmen that the root and stem of *B. sagittata* often cause stock poisoning, especially among sheep. Certain experimental proof of this toxic property of the resinic esters and the resene of this plant will be presented.

A neutral potassium resinate was prepared from titration with a saturated solution of potassium hydrate and an alcoholic solution of the resinic acid. The alcohol was allowed to evaporate and the ester dissolved in water to make a saturated solution. A few drops of this solution were introduced into a watchglass containing filaments of *Chara* in 10 cc. of tap water. Such a dilute solution of the ester was not sufficient to effect any osmotic changes in any appreciable way. Observations were made in the following manner.

A filament of *Chara* had previously been singled out and the rate of flow of the protoplasm under low power of the microscope noted. A convenient distance was chosen on a blank paper at the side of the microscope, and by means of a camera attachment the time for this distance flow was then taken to ascertain the average time flow. Such an average in this case was found to be 20 seconds, with a maximum at 22 and a minimum at 18 seconds. A final normal reading was taken at 9:14 A.M. and the specified amount of the ester introduced. Five minutes later the time flow was 30 seconds; 6 minutes later, 27 seconds; 7 minutes later, 25 seconds; 8 minutes later, 23 seconds; 13 minutes later, 23 seconds; 15 minutes later, 20 seconds; and at 10:38 A.M., 19 seconds. This shows an immediate effect in the time flow and a rather rapid recovery. When a double dose of the solution, that is, 6 drops of the

saturated solution to 10 cc. of water, was used, the following data were secured:

12:40–12:58 P.M.	Time flow 20 seconds
12:59 ester introduced	
1:00	25
1:01	30
1:02	30
2:03	35
2:04	35
4:18	40
4:22	30
4:25	32
4:26	33
4:30	30
5:00	60
5:04	60

9:00 A.M. following, death of the filament, but with no plasmolysis

Check experiments on a new filament with the same toxic doses were used, with similar results.

TRUE (**20**), working on *Lupinus albus*, found for inorganic acids that the H ion produced the greater toxic effect on the vitality than the Na ion of the sodium salt. The same was correspondingly true for organic acids, with the toxicity proportional to the dissociation of the H ion. It may be noted in passing that the resinic acid would probably be more toxic than the potassium salt.

In the process of steam distillation of the resene condensation at 10° C. is not complete. Unless the apparatus is inclosed in a hood with a good vent, the room soon becomes permeated with the volatile resene. It has a characteristically sweetish odor, very terebinthine in nature. During a period of 3–4 hours the writer was in the immediate vicinity of a resene still, with the room temperature at 22° C. and the condenser at 10°. Certain pains developed under the eyes with sharp, shooting pains in the occipital region. Also a dull pain developed in the spinal cord, mostly in the lumbar region. Within a short time a high fever arose (102–104° F.), alternating with chills. At times, as the chills abated, the blood coursed through the head, seemingly laden with fire. A tickling sensation

was produced in the respiratory tract, centering in the bronchi, giving rise to coughing which seemed almost to split the head. This condition continued for almost 36 hours, at the end of which time the fever began to abate and the acute pains to leave. The irritation of the lungs and bronchi continued for more than a week before it was relieved.

A similar test was made, except that the windows were wide open and a strong breeze blew the vapors away from the writer. No ill effects were observed. Again, when the apparatus was thoroughly hooded, no harmful effects were felt.

In steam distillation, where water and resene distil and condense simultaneously, the resene collects on top of the distilled water. It was found, however, that a fine grade of filter paper does not free the filtrate of the resene product, evidently due to a colloidal suspension of the resene in the water. When exposed to the air and allowed to evaporate for some time, some of the suspensoid is precipitated in crystal form. The toxic effect of this colloidal suspensoid of resene is brought out by the effect on the protoplasmic flow of *Chara*.

Resene was distilled from fall roots of *B. sagittata* and allowed to condense at 10° C. along with water. This water was filtered and the filtrate allowed to act on *Chara* sp. It tested tannin free. The normal time flow for a unit distance was found to be 10, 10, 10, 10, 10, 10, etc. The *Chara* was then transferred to this colloidal suspension, in parts one of the suspension to nine of water free from the suspensoid. Observations on the effect of the resene on the protoplasmic flow were made for 90 minutes. The observations are recorded in table VI.

A study of the data shows a marked lowering of the vitality immediately upon the introduction of the resene, followed by increased activity of the protoplasm. The lowering of the protoplasmic flow occurred almost rhythmically, followed by an alternate rhythmic increase in vitality. This continued until the final decrease in flow, with death ensuing. The amount introduced was much less than that required for an appreciable exosmosis (text fig. 2).

The writer recognizes that a correct quantitative measurement of the toxicity of resene and resinic esters is desirable, and has under

way such a test, together with a physiological standardization of the products.

TABLE VI

RECORD OF EFFECT OF COLLOIDAL SOLUTION OF RESENE FROM *B. sagittata* ON PROTOPLASMIC FLOW OF *Chara* SP. THROUGH UNIT DISTANCE OF 0.465 MM.

Time	Time flow	Time	Time flow	Time	Time flow
7:15 P.M.	10	7:41 P.M.	18	8:09 P.M.	12
7:16	10	7:42	No record	8:10	13
7:17	10	7:43	13	8:11	14
7:18	10	7:44	12	8:12	15
7:19	10	7:45	8	8:13	14
7:20*		7:46	8	8:14	No record
7:21*		7:47	10	8:15	"
7:22*		7:48	10	8:16	13
7:23	15	7:49	12	8:17	13
7:24	15	7:50	12	8:18	13
7:25	16	7:51	14	8:19	19
7:26	14	7:52	18	8:20	20
7:27		7:53	13	8:21	15
7:28	10	7:54	18	8:22	14
7:29	8	7:55	18	8:23	14
7:30	6	7:56	22	8:24	No record
7:31	12	7:57	23	8:25	"
7:32	15	7:58	28	8:27	18
7:33	12	7:59	22	8:28	No record
7:34	10	8:00	18	8:29	14
7:34.5	8	8:01	13	8:30	11
7:35	15	8:02	12	8:31	14
7:35.5	20	8:03	12	8:32	12
7:36	17	8:04	12	8.33	15
7:37	16	8:05	14	8:34	24
7:38	14	8:06	11	8:35	∞ with death
7:39	14	8:07	No record		
7:40	18	8:08	16		

*Resene introduced here.

Discussion

A survey of the study of resin secretion makes it evident that the problem can be considered logically only in the light of the threefold evidence, the ecological, the anatomical, and the physiological. The assertion of TSCHIRCH (*loc. cit.* p. 1145) that "we shall assuredly not arrive at a conclusion by anatomico-microchemical" investigations is only a half truth. All phases of the problem must be carefully weighed in order to understand the problem. In this evidence the anatomico-microchemical data surely have their place.

The writer does not claim that the particular solution of resin secretion for *B. sagittata* is a complete solution for resin secretion

in all plants. However, it suggests a method of attack to be followed in working out other problems of a similar nature and scope.

The problem of resin secretion in *B. sagittata* is one limited to the field of an acid resin, non-tannin testing. For this type of resin, perhaps by far the most common, theories have been advanced

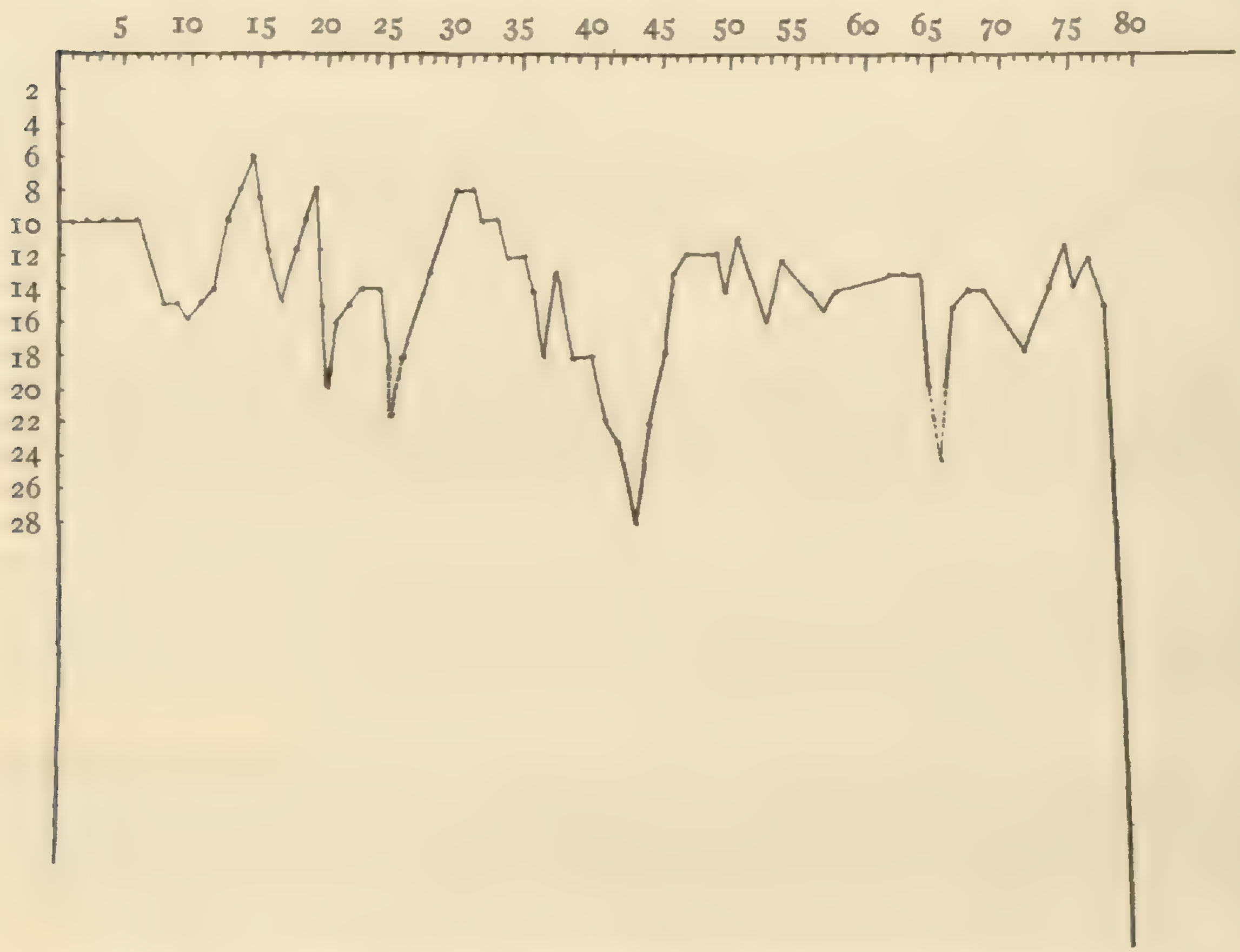

FIG. 2.—Coordinate plot, representing effect of balsamoresene on protoplasmic activity of *Chara* sp; the ordinates represent time flow and abscissas sequence of time.

advocating the origin from carbohydrates on the one hand, and the origin from terpenes on the other. Foremost of those advocating the former theory was WIESNER (**24**). He assumed that resins are derived from carbohydrates, specifically starch, by polymerization and reduction. As he knew, this fails to account for resin in the pine family, where there is a maximum production of resin but very little starch formation. WIESNER explained this on the basis that gallo-tannic acids operated to produce the change in this family.

Recently FRANKFORTER (5), working from the biochemical angle, has criticized WIESNER'S theory on the ground that it is unreasonable to suppose a complex starch molecule would be formed and then broken down into the terpene and resene radical. The criticism is not well founded, because it fails to consider the fundamental function of resin secretion. In other words, this criticism evades the anatomico-physiological viewpoint which TSCHIRCH claimed could never solve the problem; but in evading this point of view the entire meaning of resin secretion is overlooked.

The theory of resin formation from terpenes is supported both by theoretical and actual evidence. Such a theory was postulated by BAEYER (1), who obtained several resins by oxidation of fatty aldehydes, although these resins were unlike any found in nature.

The evidence presented from a biochemical study of *B. sagittata* shows (1) the presence of a resinic acid, with reaction similar to that for abietic acid; (2) production of the fatty aldehyde, *balsamoresene*, by steam distillation of the resinic acid and the formation of the resinic acid from resene in the presence of oxygen; and (3) a strong test for inulin, a polysaccharide, in photosynthetic and conductive areas, in conjunction with balsamoresene. This evidence, added to the comparative studies, warrants the assumption that *balsamoresinic acid is derived from balsamoresene*, which, in turn, is derived from inulin by polymerization.

Although the evidence already presented in the physiological section is the most convincing, yet that secured from the ecological data and anatomical observations brings the problem to a clearer focus. HABERLANDT (*loc. cit.* p. 525), referring to the coincident bundle traces and secretory canals, concludes that "the reason for the frequent association of secretory passages with leptome strands and other vascular tissues is, therefore, in all probability, an ecological one." Furthermore, "the substances contained in these passages are often of such a kind as to be capable of affording 'chemical protection' against noxious animals; hence small assailants which have penetrated into the interior of an organ will be more or less effectually discouraged from attacking the conductive strands, the continuity of which is so vital to the well-being of the

plant, if the latter are protected by a series of secretory ducts (or excretory sacs)."

A criticism of this theory lies in the fact that it fails to comprehend the origin of resin per se, and tries to explain its reason for existence *ab exteriore*. The ecological evidence from *B. sagittata* would discourage any such reason for resin secretion. As has been described, diptera, acarinids, and nematodes parasitize the growing and reproductive parts of the plant. The fly nymph lays the eggs between the parts of the flower head, where the grub hatches and worms its way through the tissue, irrespective of resin canals, effectually limiting the source of nourishment of the ripening seeds and causing a high percentage of non-viability. The mites suck the juices of the conductive tissue, especially at the bases of the new stems and petioles, where there is an abundance of resin in the tissues. The nematodes bore into the conductive tissues of the leaf and bud and cause a withering and decay right in the resin secreting areas.

Another ecological reason assigned for resin secretion is its protection against mechanical injury to cortex. It is based on the ground that such injured places are often covered by a resin covering. Undoubtedly this is often true, but it must be considered a secondary function, not at all the fundamental reason for resin secretion.

The fundamental underlying reason for resin secretion lies in the essential toxic nature of the resin to the plant itself. The resin is a by-product, formed in the metabolic activities of the plant. It is harmful to the plant, as judged from its effects on other organic tissues and from the storage of the product within special tubes or canals in the endodermal region, near to the place of greatest activity and growth. Since these resene and resinic acid products are toxic, they may be used as a guard against mechanical and parasitic injury. They may or may not be effective in such capacity.

Moreover, the anatomical observations verify this hypothesis. The balsamoresinic acid and the balsamoresene develop in cambium and other meristematic regions. They are carried outward by the rays and phloem strands until they reach the resin canals, where

they are laid down. Such seems to be the significance of the penetration of the phloem strands into the cortical areas through the Casparian strip (fig. 13).

Much emphasis has been placed by TSCHIRCH (*loc. cit.* p. 1118) on the non-permeability of resinic acid through cell walls. This author contends that resin is laid down where it is formed. Yet in an alkaline medium, such as is frequently if not always found in growing tissues, an unstable resin ester would be formed, undoubtedly capable of penetrating cell walls. Then, too, the fact remains that a considerable part of the resin forms in the meristem and is transferred to the canals, else it would never get to the canals. Such a transfer could be accomplished in the form of a temporary ester. On the other hand, the microchemical observations show that the larger amount of the product is transferred as balsamoresene and changed to the acid in the vicinity of the cells immediately surrounding the canals or in the canals themselves. There is even evidence to support the view that inulin may be changed into resene and later into resinic acid in the vicinity of the canals. In fact, such a change is actually shown in progress in fig. 36. There seems to be no specific way for the translocation of the by-products to the resin ducts. It may be accomplished by a temporary ester formation, or by the translocation in the form of balsamoresene, and later changed into resinic acid, and it may be centrifugally distributed as a fractional depolymer of inulin, and consequently changed to resene and resinic acid near the canals. Any one of these means would satisfy the needs of a translocation in a dialyzable form.

Summary

1. *Balsamorrhiza sagittata* is the dominant member of its habitat in the inter-mountain region. The plant depends largely upon growth of the rootstock for propagation. It does not produce flowers until the third or fourth season. A hardy rootstock accounts for its dominance, since the viability of the seeds is small, due to parasitic infection.

2. The radicle has the tetrarch type of development. The resin canals of the root arise in two concentric rows above and

including the hardy mid-rootstock, with radial canals between the longitudinal canals of the two series. Only the outer of the two series of canals is found in the lowest portion of the rootstock and the subsidiary roots. A twofold series of canals is found in the stem and leaves, an outer series in the sinuses of the cortex opposite the interfascicular regions, and a second inner series in the pith opposite the hadrome elements. The root canals and the stem canals arise as two separate systems and remain distinct. The resin canals do not arise until long after resin is formed in the meristem.

3. *Balsamoresene* and *balsamoresinic* acid are formed in *B. sagittata* from *inulin*, probably by polymerization and reduction. The resene and resinic acid are essentially toxic in nature. The resene is the immediate substance from which resinic acid is formed. The secretory process is dependent on physiological activity in the meristem of the plant, in which inulin is used in anabolism and resene and resinic acid are derived as waste products in the plant. The resinic acid and resene are transferred to the secretory canals, where they are stored.

4. To summarize, the study of *B. sagittata*, with especial emphasis to the meaning of resin secretion, has developed certain facts regarding the purpose of resin secretion. In the growth of the plant a polysaccharide, inulin, produced during photosynthesis, is broken down, causing a by-product, balsamoresene, to be produced. This resene is changed to resinic acid. On account of the probable toxic nature of the resene and resinic acid to the plant, they are translocated to schizogenously formed ducts of endodermal origin, where they are stored as resinic acid.

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EXPLANATION OF PLATES XXVIII–XXXI

FIGS. 1–6.—Successive stages in germination of seeds of *Balsamorrhiza sagittata:* fig. 1, seed coat bursting, with hypocotyl protruding, 15 days' growth; figs. 2–5, stages from 20 to 40 days' growth; fig. 6, stage showing 60 days' growth; note type of venation in plumule; figs. 1–5, ×1.5; fig. 6, ×1.

FIGS. 7–10.—Successive stages in development of bundle anatomy of seedlings: fig. 7, formation of protoxylem, other tissues yet undifferentiated; fig. 8, protoxylem (*px*) well defined, rapid differentiation of procambium (*pc*) in region where protophloem originates; fig. 9, rapid division of cambium to form secondary xylem elements (*mx*) and phloem (*ph*); fig. 10, suberization of endodermis (*en*) beginning, secondary xylem, the metaxylem, well differentiated; ×112.

FIG. 11.—Gradation of tracheids from spiral protoxylem to true eyelet type of metaxylem; taken in region of fig. 10; ×150.

FIG. 12.—Detail of suberized walls in region of endodermis, defining "H" type of thickening: *ex*, toward cortex; *in*, toward leptome.

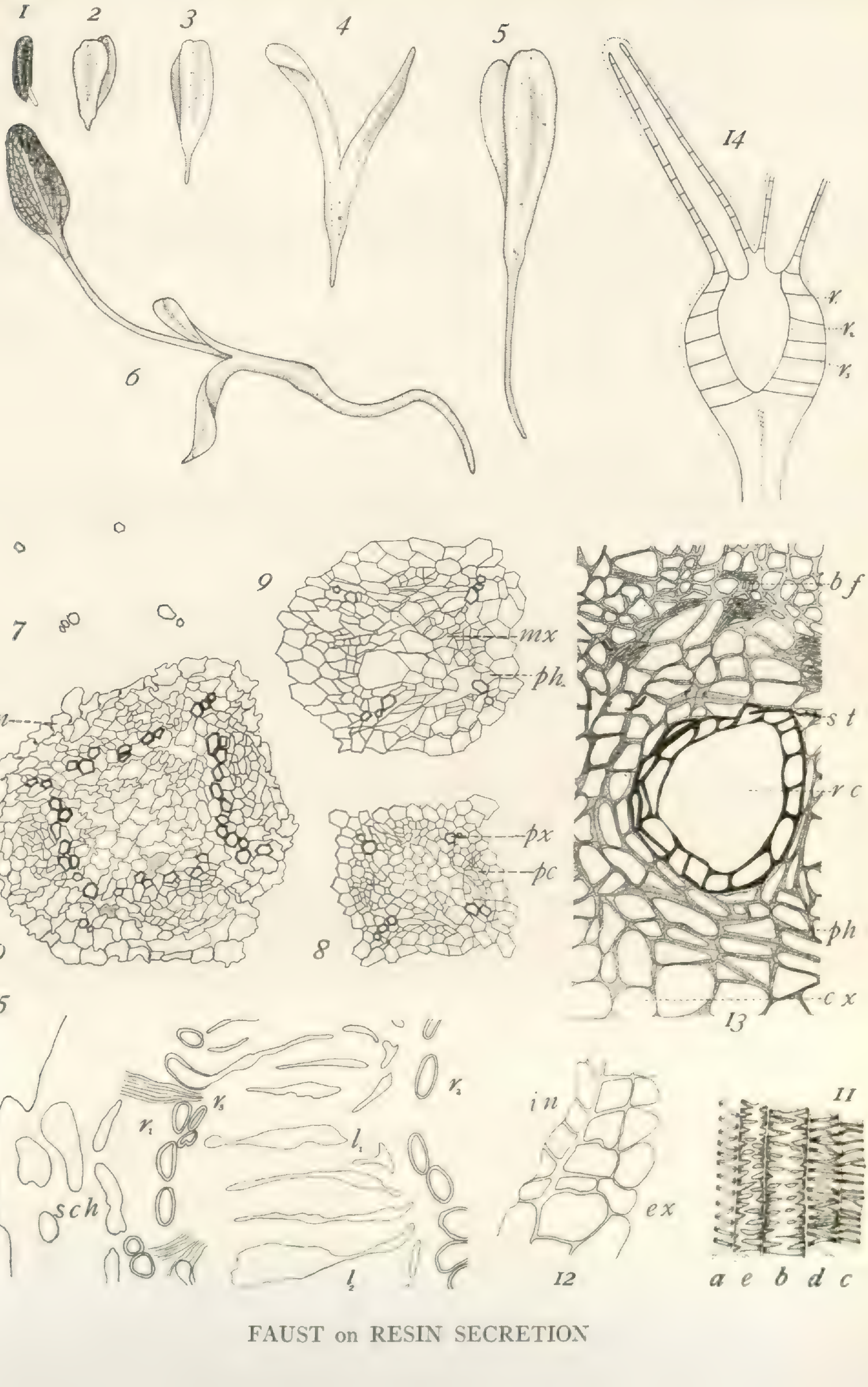
FIG. 13.—Section through 10 mm. root, illustrating passage of phloem strands through endodermis into cortex in region of canals: *ph*, phloem cells; *rc*, resin canals; *bf*, strands of bast fibers; *cx*, cells of cortex; *st*, suberized thickening of endodermis; ×150.

FIG. 14.—Diagram of resin canals in longitudinal section through stout rootstock and root branches: r_1, outer series of canals; r_2, inner series of canals; r_3, anastomosing radial connections; note inner series ends in stele just above tap root; ×0.75.

FIG. 15.—Transverse section through old root: r_1, outer series of canals; r_2, inner series of canals; r_3, radial connections; *sch*, sclerome groups; l_1, l_2, lysigenous splittings of rays; ×150.

FIG. 16.—Section through young subsidiary root with stele yet unsclerified, showing bundle anatomy: *px*, protoxylem; *cx*, cortex; *hyp*, hypodermis; *e*, epidermis; note deposits of inulin in granular masses; type of root readily permeable to alcohol; ×150.

FIG. 17.—Section through subsidiary root with moderate thickenings; note suberization of endodermis, rapid division of cambium, metaxylem ele-



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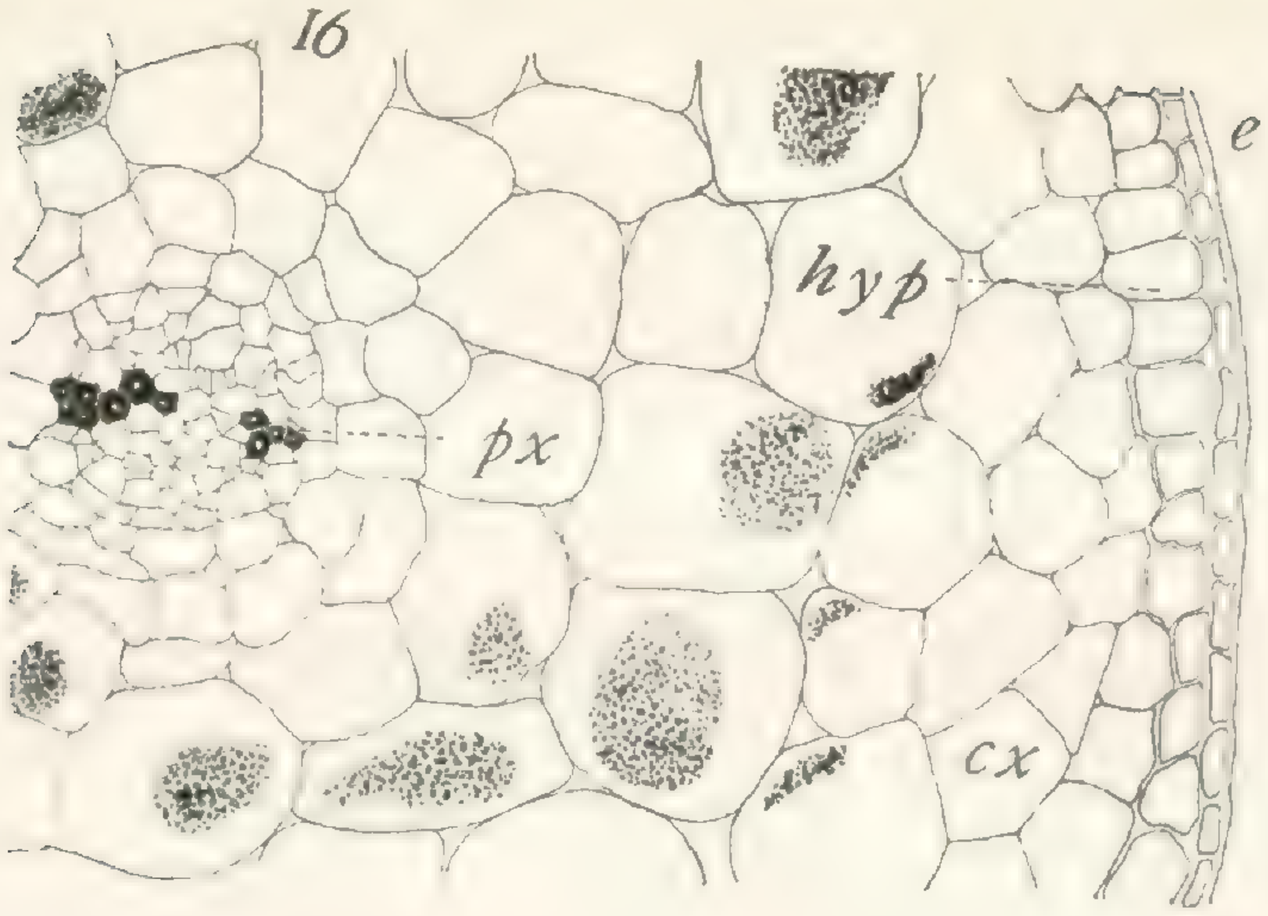

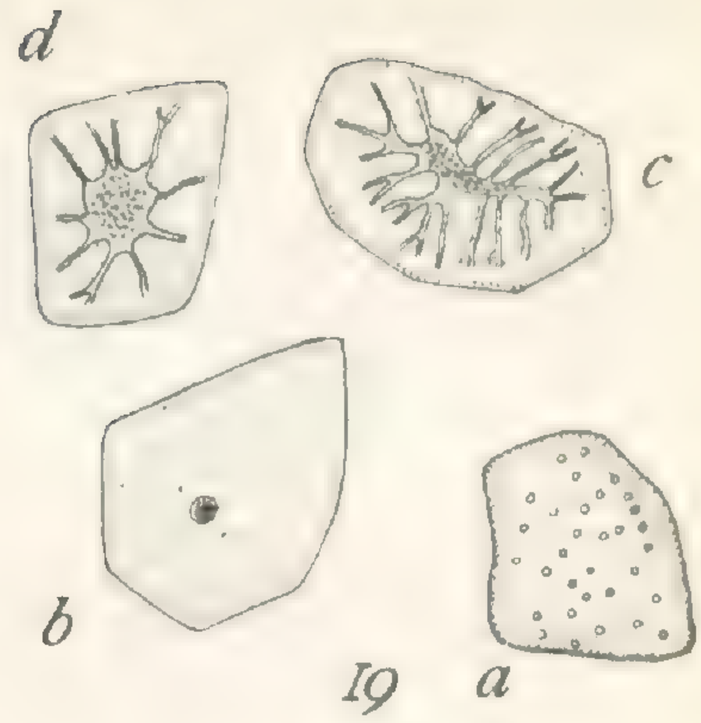

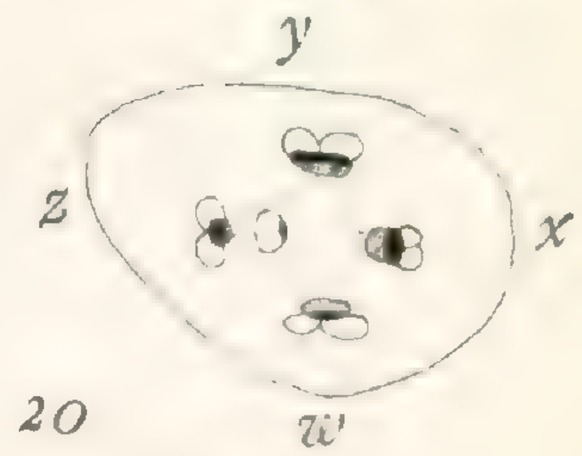

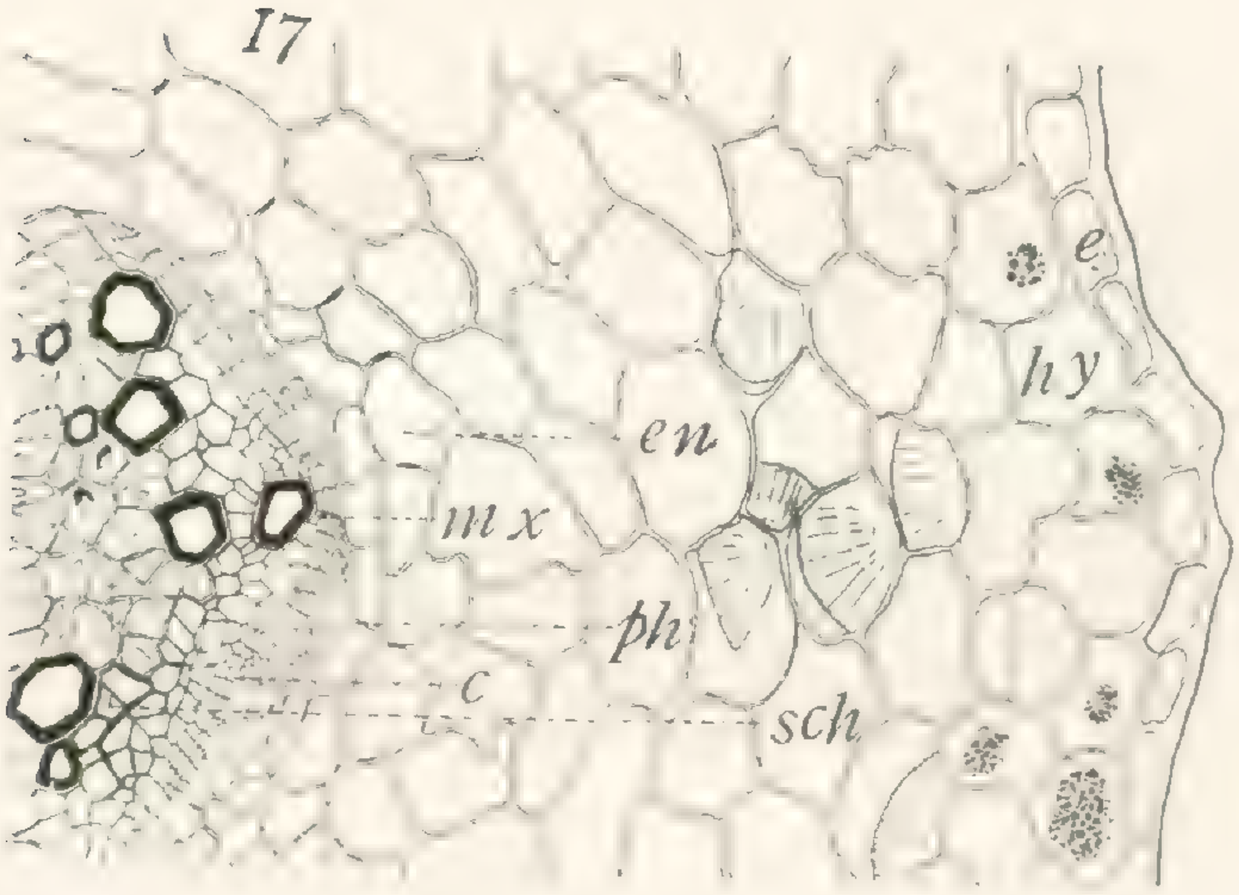

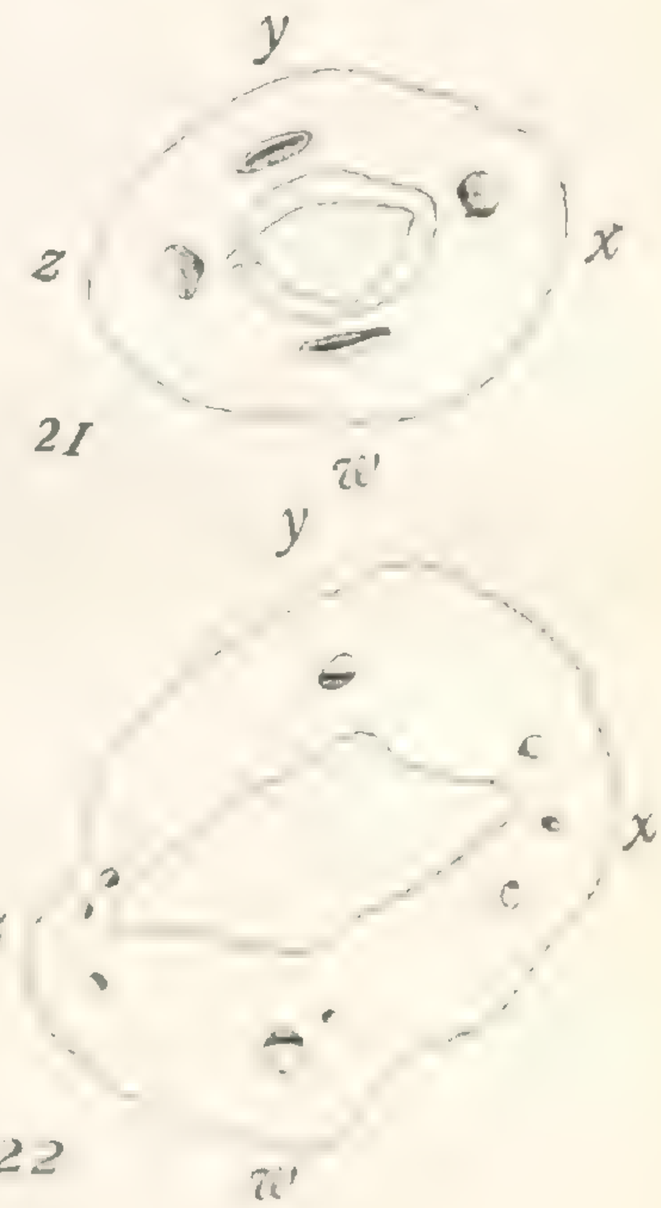

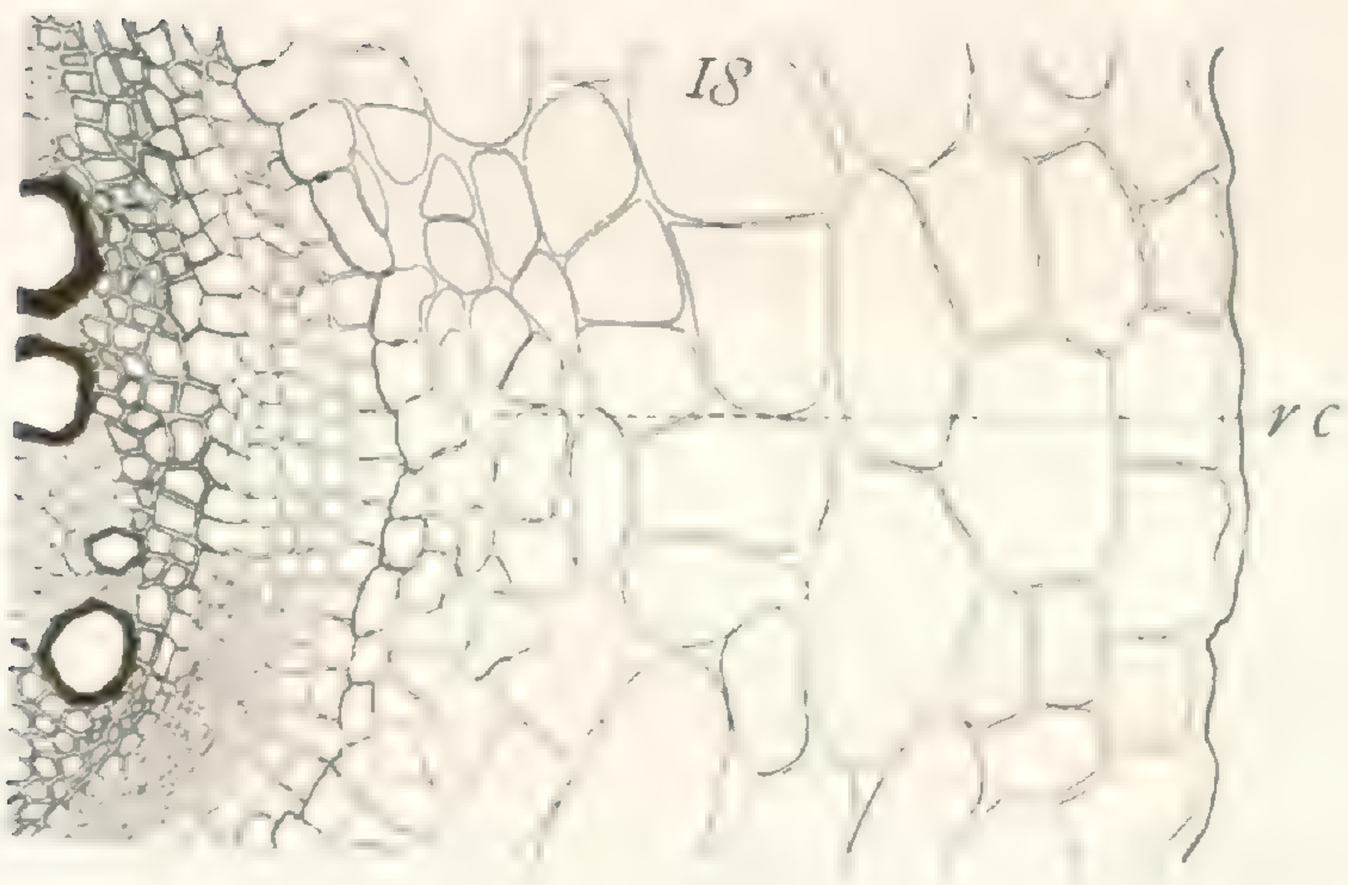

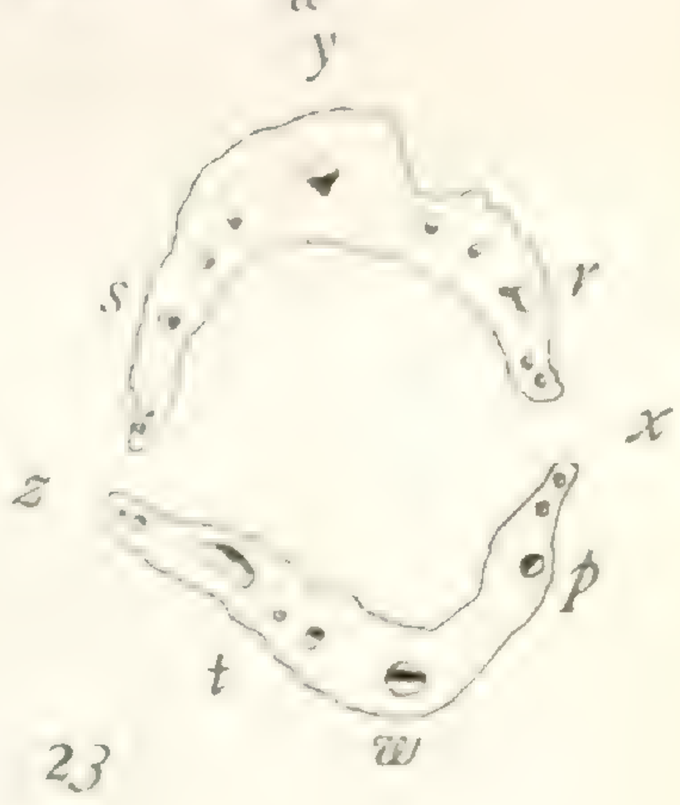

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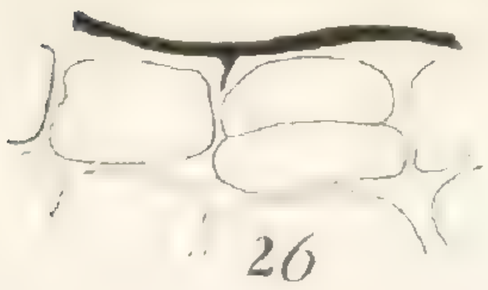

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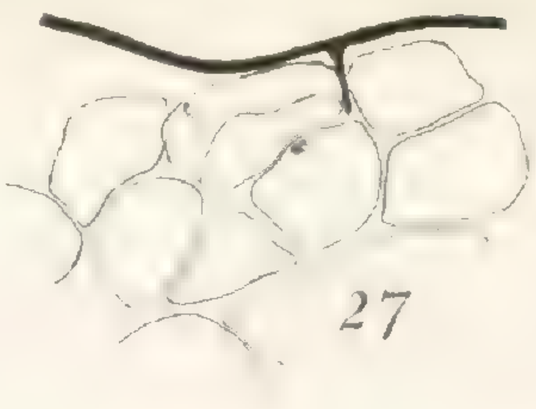

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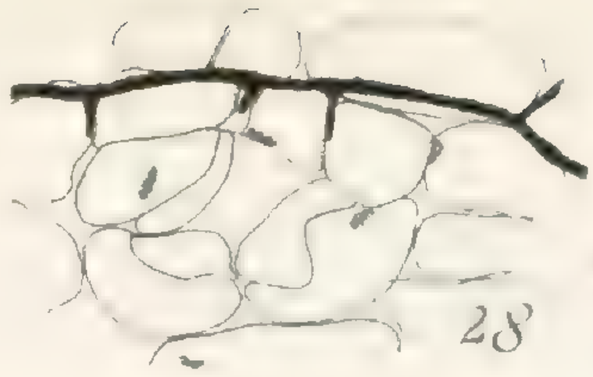

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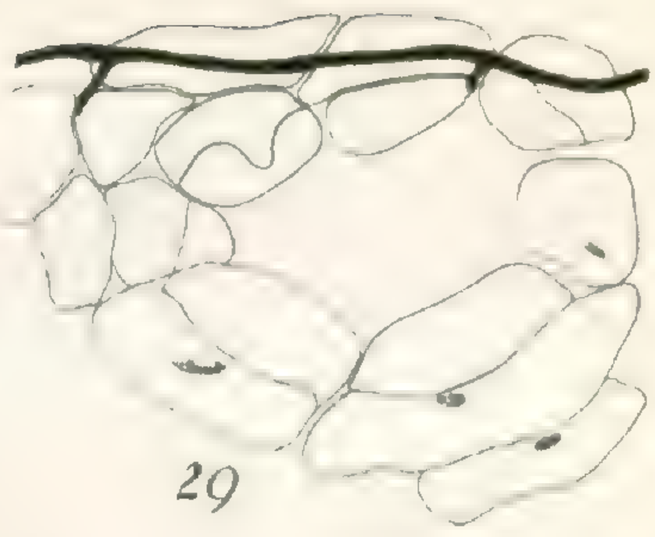

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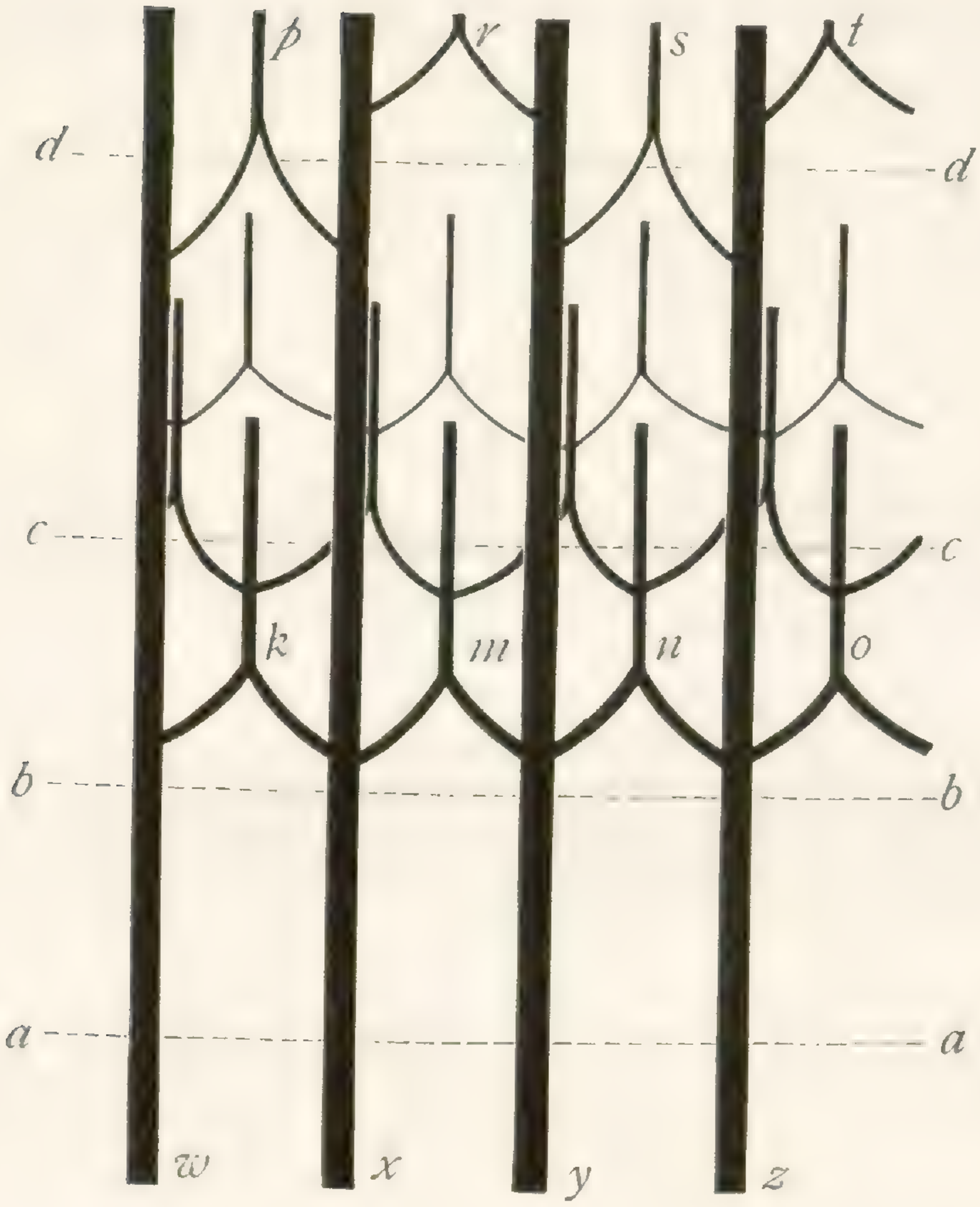

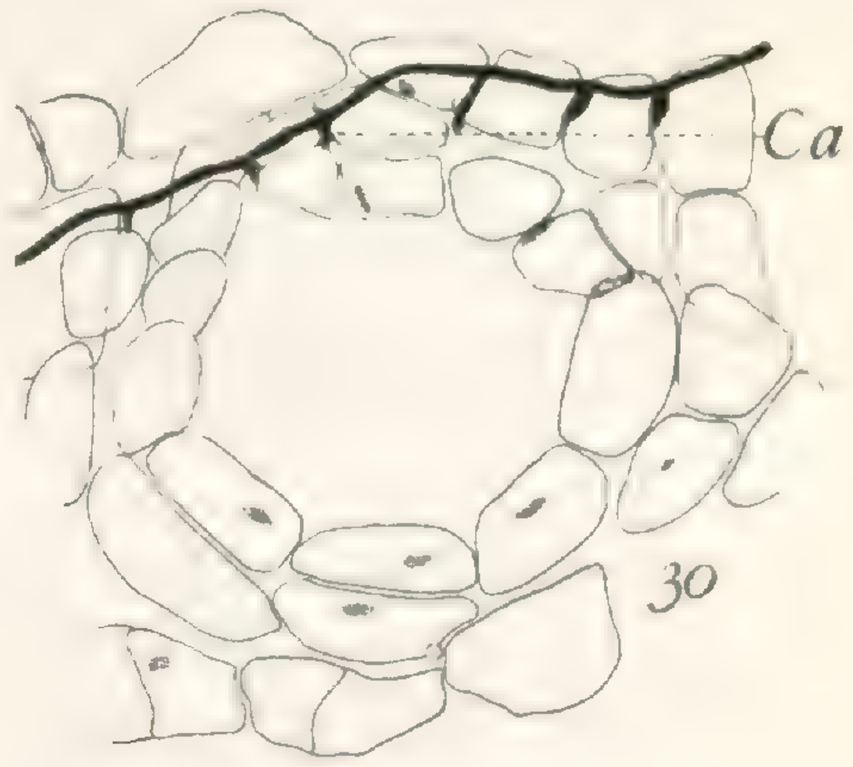

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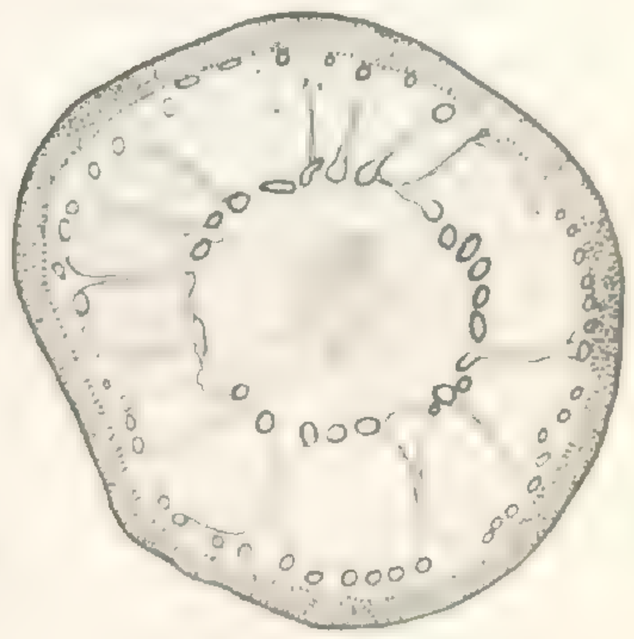

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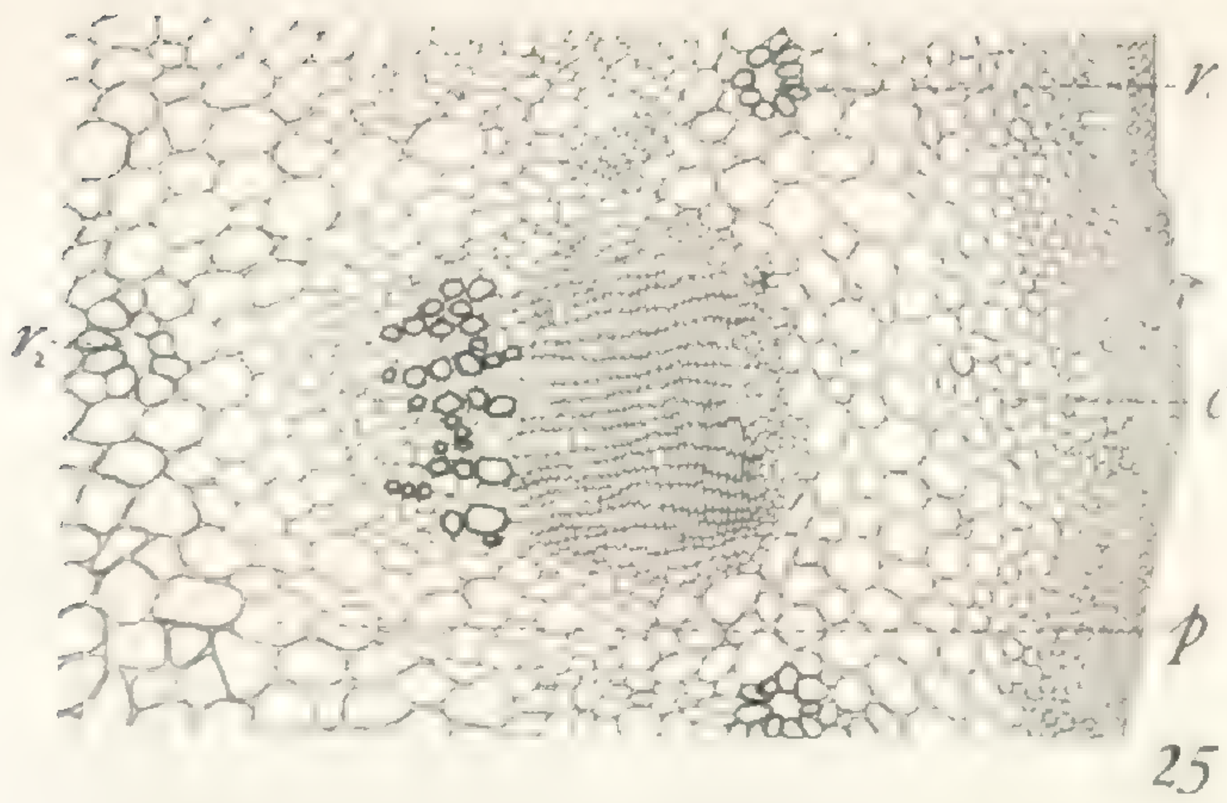

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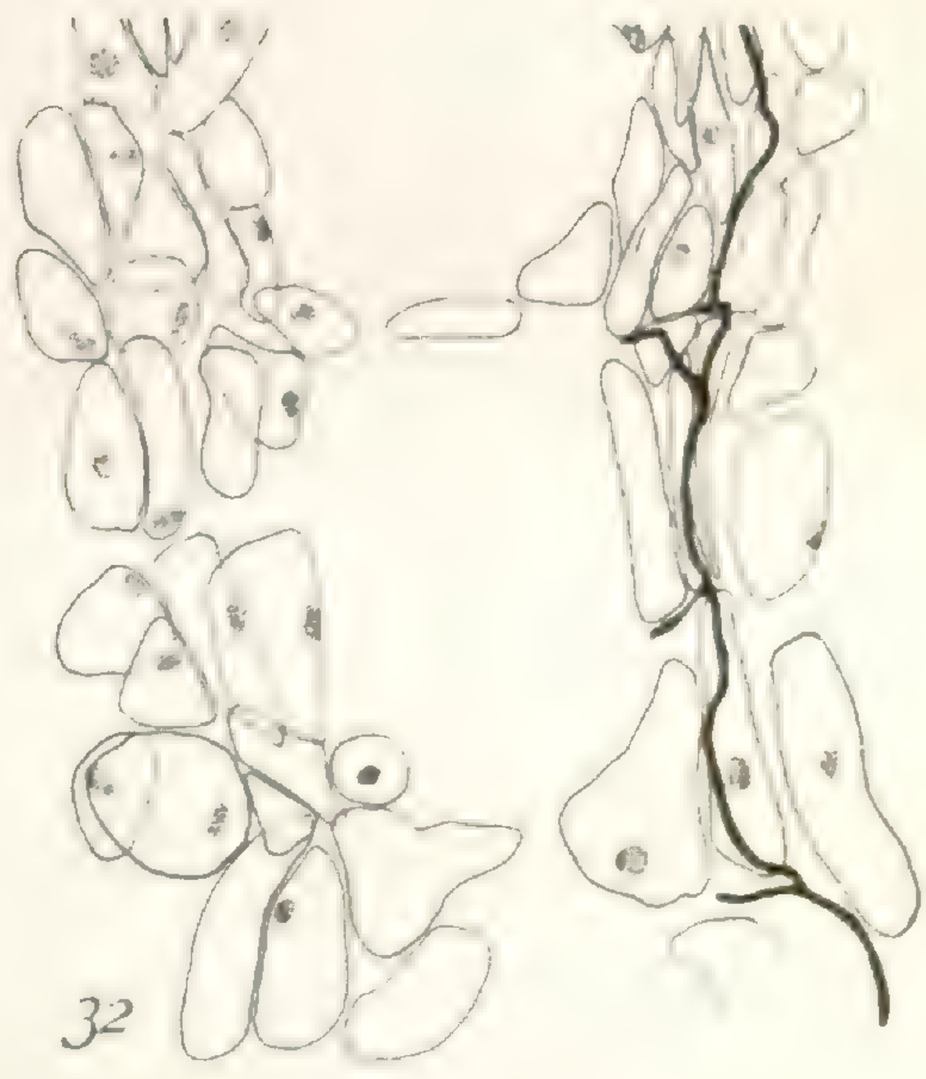

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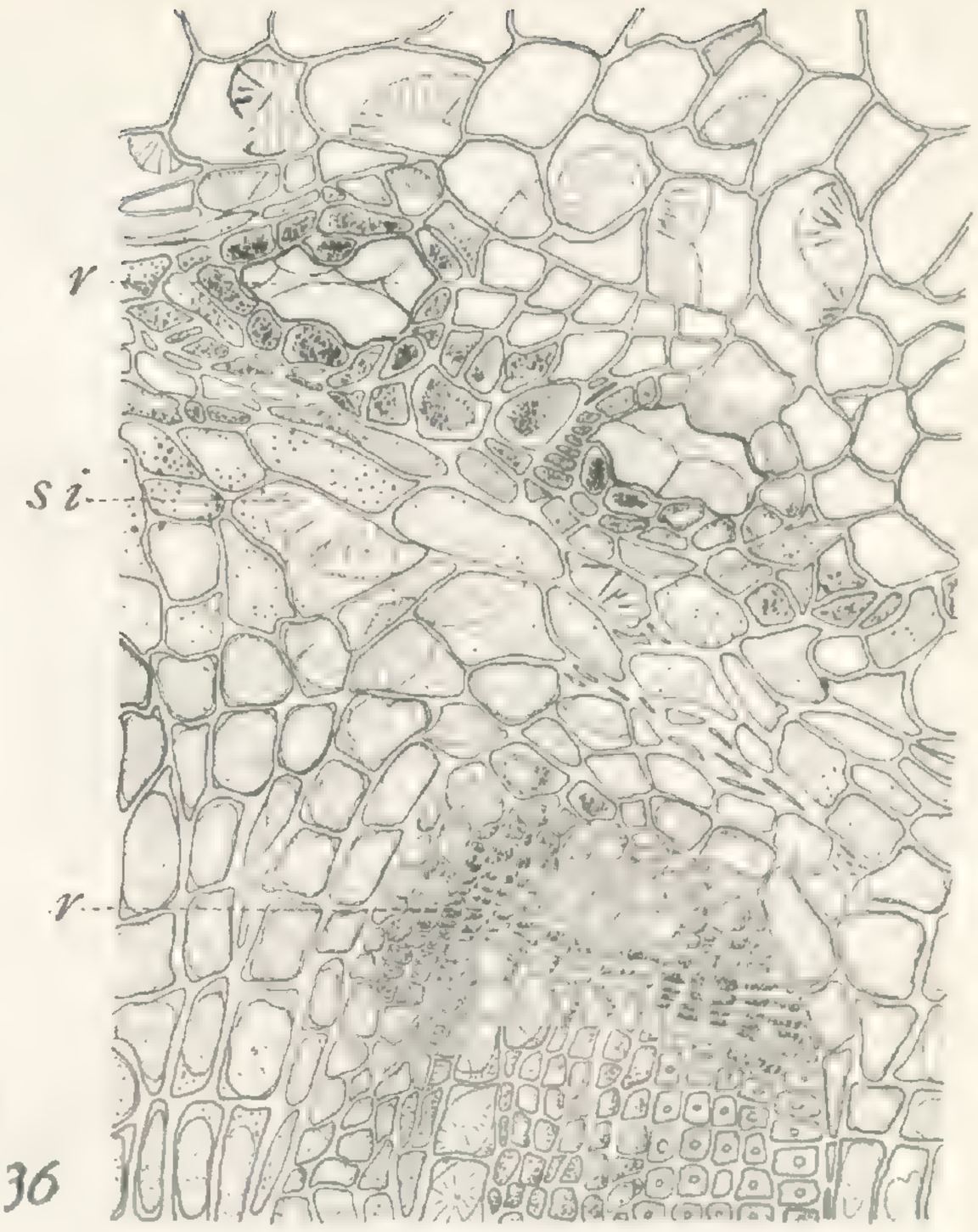

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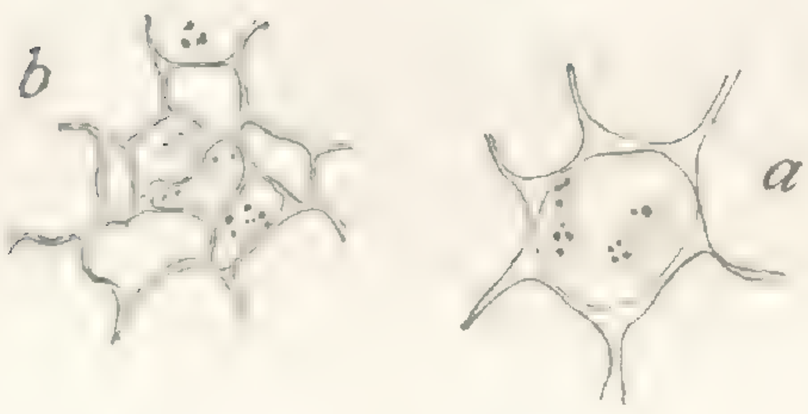

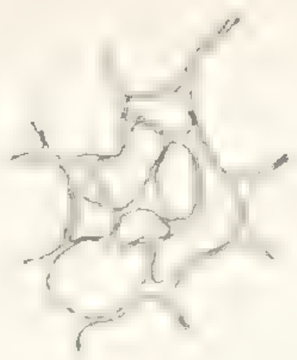

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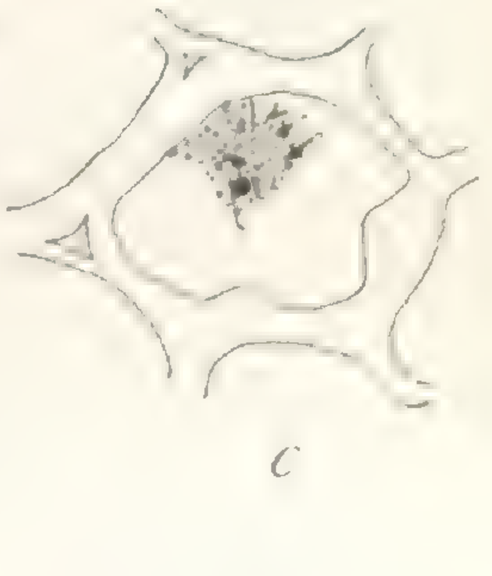

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ments, and sclerified stele; inulin deposits in outer cortex granular; in inner cortex, sphero-crystals; *mx*, metaxylem; *ph*, phloem; *c*, cambium; *sch*, sclerome; *en*, endodermis; *hy*, hypodermis; *e*, epidermis; ×150.

FIG. 18.—Section through old subsidiary root, showing formation of resin canals in region of endodermis: *rc*, resin canals; ×150.

FIG. 19.—Detail of sections of stone cells: *a*, section at edge of cell showing unsclerified pores; *b*, border of internal opening; *c*, *d*, through center of cells; *a*, *b*, *d*, longitudinal sections; *c*, transverse sections; ×300.

FIGS. 20–23.—Sections through critical levels of a 2 mm. seedling: fig. 20, region of hypocotyl; fig. 21, lower cotyledonary collar; fig. 22, upper cotyledonary collar; fig. 23, lower reaches of cotyledons; *w*, *x*, *y*, *z*, primary bundle traces in hypocotyl; *p*, *r*, *s*, *t*, secondary bundles of cotyledonary collar; white areas in bundles, phloem; black areas, xylem; dotted areas, metaxylem; ×60.

FIG. 24.—Longitudinal diagram of bundle traces in region of hypocotyl and lower epicotyl, reduced to one plane: *k*, *m*, *n*, *o*, primary traces of epicotyl; other designations as in figs. 20–23.

FIG. 25.—Transverse section through peduncle: *p*, pith; *c*, cortex; r_1, resin canals of outer series; r_2, resin canals of inner series; ×150.

FIGS. 26–30.—Cross-sections of resin canals of root at various stages of development: fig. 26, first periclinal division of initial endodermal cell; fig. 27, first oblique division; figs. 28, 29, progressive stages in formation; fig. 30, fully developed canal; *Ca*, Casparian thickening; ×150.

FIG. 31.—Transverse section of old root (4 or 5 years), showing two series of canals and radial anastomoses; ×1.

FIG. 32.—Longitudinal radial section of fully developed canal; ×150.

FIG. 33.—Transverse section of young seedling in hypocotyledonary region, showing radial anastomoses of two series of resin canals in root system: r_1, outer series; r_2, inner series; *a*, radial canals.

FIG. 34.—Schematic diagram from sections, illustrating extent and connections of resin canals of 5 mm. seedling, in region of hypocotyl: r_1, outer series of canals; r_2, inner series of canals; *a*, radial canals.

FIG. 35.—Section through origin of resin canals of stem: *a*, initial canal cell in process of division; *b*, cells dividing a second time; *c*, *d*, subsequent divisions to form canals; ×300.

FIG. 36.—Section of 3-year-old root, stained to show distribution of inulin and resin: *si*, sphero-crystals of inulin; *r*, *r*, resin deposits.

FIG. 37.—Detailed sketch of inulin, resene, and resinic acid: *a–d*, within pith cell of stem; *e*, *f*, deposited from evaporation of alcoholic solution; *a*, crystal of inulin; *b*, crystals of resene within cell; *c*, *d*, resene crystals imbedded in resin masses; *e*, detail of resene crystal; *f*, resene crystal imbedded in resin masses; ×150.

DISTINGUISHING CHARACTERS OF NORTH AMERICAN SYCAMORE WOODS

WARREN D. BRUSH

(WITH PLATES XXXII–XXXVIII AND THREE FIGURES)

Native sycamores[1]

Four out of the five known species of sycamores (*Platanus*) are natives of North America. One of these is found in the eastern United States, one in the southwest, one in the Pacific Coast region, and one in Mexico. The only species in the Old World inhabits central and southern Europe and southwestern Asia. The North American species are the common sycamore (*P. occidentalis* L.), California sycamore (*P. racemosa* Nutt.), Arizona sycamore (*P. Wrightii* S. Wats.), and the Mexican sycamore or alamo (*P. Lindeniana* Mart. and Gal.). The oriental plane tree (*P. orientalis* L.) is perhaps the most widely known as well as one of the largest trees in the temperate climate and is frequently planted for shade in streets and parks.

Gross structure

The only sycamores considered in this paper are the three species native to the United States: the eastern or common, the California, and the Arizona sycamores. The woods of these native sycamores so closely resemble each other in general appearance that

[1] The name sycamore rightly belongs to a fig tree (*Ficus sycomorus* L.), a native of Asia Minor. Sycamore is a combination of two Greek words, *sykon*, a fig, and *moron*, a mulberry. The leaves of this oriental fig tree resemble those of a mulberry. In Australia this name is applied also to *Panax elegans* F. and M. and *Sterculia lurida* F. and M. In France the name *faux sycomore* is given to the China-tree (*Melia Azedarach* L.). The name is popularly applied in this country to sycamore maple (*Acer pseudo-platanus* L.), because of a general resemblance of the leaves. Plane tree is the generally accepted name for the oriental *Platanus orientalis*, and it has been applied to the North American *P. occidentalis* from early times. The names applied locally, however, are buttonball, buttonwood, cottonwood, and water beech. Buttonball is a suitable name because it has not been applied to any other tree, and it is descriptive of the fruit. Sycamore is the accepted trade name and the one most widely used.

the elements which serve as distinguishing characters must be magnified, to some extent at least, for positive identification. The chief distinguishing characters of the sycamore woods are the color of the sapwood and heartwood and the size of the pith rays. The average weight[2] and hardness of these woods differ very little, and hence they cannot be depended upon as distinguishing characters. Specific gravity and the weight per cu. ft. are shown in table I.

TABLE I

Species	Specific gravity	Weight in lbs. per cubic foot
Platanus occidentalis.....	0.5678	35.39
Platanus Wrightii.....	0.4736	29.51
Platanus racemosa.....	0.4880	30.41

SAPWOOD AND HEARTWOOD

While the sapwood and heartwood usually do not show distinct limits, they are easily distinguishable from one another by their color. The sapwood of the eastern sycamore is light brown, and the heartwood has a decidedly reddish tinge; the sapwood of California and Arizona sycamores is a yellowish white, while the heartwood is somewhat darker and only slightly tinged with red. In all species the sapwood occupies only a thin zone. Both the color and thickness of the sapwood and heartwood, however, are very variable, depending probably to some extent upon the age, climate, soil conditions, and the general health of the tree. Trees growing in low or moderately wet soil usually develop thicker sapwood than those found on higher well drained ground. As a rule the eastern species has a thicker sapwood than the western ones.

ANNUAL RINGS OF GROWTH

Annual rings of growth in all three species (pls. XXXII–XXXIV, *ew* and *lw*) are clearly visible to the unaided eye. Each ring is defined from the next layer by a more or less distinct

[2] The Hardwood Manufacturers' Association has determined the weight of eastern sycamore lumber to be 3200 pounds per 1000 board feet. The weight per board foot of the western species has not been listed.

tangential line made up of several rows of radially flattened wood fibers which mark the outer boundary of the late wood. The early wood of the next annual ring lies immediately outside of this dense tissue, and it begins with a more or less continuous row of pores. The portion of the ring formed in the beginning of the year's growth is thus considerably more porous than that produced at the end of the season. The pores are slightly less numerous and smaller in diameter in the late wood than in the early wood, but they are so nearly uniform in size throughout the annual rings of growth that with the unaided eye they do not materially assist in defining the inner and outer boundaries of growth rings.

The annual rings do not differ in the three sycamores except that in the eastern species they are less clearly defined than in the other two. The width of these annual layers of growth varies considerably. The annual diameter increment of the eastern species for trees of about 90 years of age and growing under average soil and site conditions is approximately 0.2 in. per year. On an average the western species grow much more slowly.

PITH RAYS

The numerous broad pith rays constitute the most striking character of sycamore wood; they are conspicuous (pl. XXXII, *pr*) both in the transverse and radial sections. In the distinctness of its pith rays sycamore woods have a general resemblance to beech, the large pith rays of the latter, however, being less numerous. The rays of sycamore wood are very conspicuous in quarter-sawed boards, giving the cut surface a "silver grain" effect similar to quarter-sawed oak. In tangential or "bastard cut" boards the pith rays are least conspicuous, although clearly visible to the unaided eye. With the hand magnifier they appear as numerous and evenly distributed, short, vertical lines.

As stated, the size of the pith rays is one of the chief distinguishing characters of the sycamore woods. In gross structure (as seen with the hand lens) the rays are decidedly larger and usually darker in the common sycamore than in the other two species.

Minute structure

The pith rays are the only reliable means for identifying the woods of the sycamores. As viewed in the tangential section, the pith rays are broadest horizontally in the common sycamore and narrowest in the California species; the rays are lowest vertically in the common sycamore and highest in the California species. The rays of the Arizona sycamore are intermediate in character. These characters can readily be seen under the microscope.

VESSELS

The wood of the sycamores is diffuse porous, that is, the pores or vessels are of approximately the same size and more or less evenly distributed throughout the annual ring of growth. They are often grouped, and together they constitute about one-half of the transverse area between the pith rays. In outline these pores are irregular and may be oval, elliptical, or nearly round; the sides in contact with other vessels are usually much flattened. The vessels first formed in the spring are usually compressed tangentially. Average diameters were computed from 50 measurements on each of the 3 species, and show very little variance (table II).

TABLE II

AVERAGE, MAXIMUM, AND MINIMUM DIAMETER OF VESSEL SEGMENTS OF THE THREE SPECIES

Species	Average	Maximum	Minimum
Platanus occidentalis.....	0.083 mm.	0.101 mm.	0.063 mm.
Platanus Wrightii.....	0.076	0.094	0.039
Platanus racemosa	0.073	0.093	0.062

The vessels are thin-walled and are composed of numerous short segments placed end to end. The upper and lower ends of these segments are usually slanting, the oblique end always facing the pith rays. In tangential or radial section these segments are readily measured under the microscope; table III gives averages computed from 25 measurements on each species.

TABLE III

AVERAGE, MAXIMUM, AND MINIMUM LENGTHS OF VESSEL SEGMENTS OF THE THREE SPECIES

Species	Average	Maximum	Minimum
Platanus occidentalis	0.786 mm.	0.889 mm.	0.718 mm.
Platanus Wrightii	0.549	0.727	0.390
Platanus racemosa	0.677	0.749	0.608

WOOD FIBERS

These elements form the ground mass of sycamore wood, and their walls are usually much thicker than those of other wood elements. The fiber length does not differ very much for the three species. They are shortest in *Platanus racemosa* and longest in *P. Wrightii*, but the difference is so slight that it cannot be depended upon as a reliable distinguishing character. Table IV gives the average lengths of 100 measurements on each species.

TABLE IV

AVERAGE, MAXIMUM, AND MINIMUM LENGTHS OF FIBERS OF THE THREE SPECIES

Species	Average	Maximum	Minimum
Platanus occidentalis	1.63 mm.	2.02 mm.	1.39 mm.
Platanus Wrightii	1.69	2.02	1.47
Platanus racemosa	1.55	1.93	1.26

TRACHEIDS

The tracheids of sycamore wood (pls. XXXII–XXXIV, *t*, and fig. 1, *E*) are found usually adjacent to vessels. These elements, together with the wood parenchyma fibers, form more or less continuous irregular lines throughout the masses of wood fibers, from which they may be distinguished by their thin walls. Tracheids take an intermediate position in respect to size and form between vessels and wood fibers, and in sycamore wood they often possess characters belonging to either one or the other of these two very dissimilar kinds of elements. About midway between these two extreme forms (the vessel and the fiber) is the more or less fixed form,

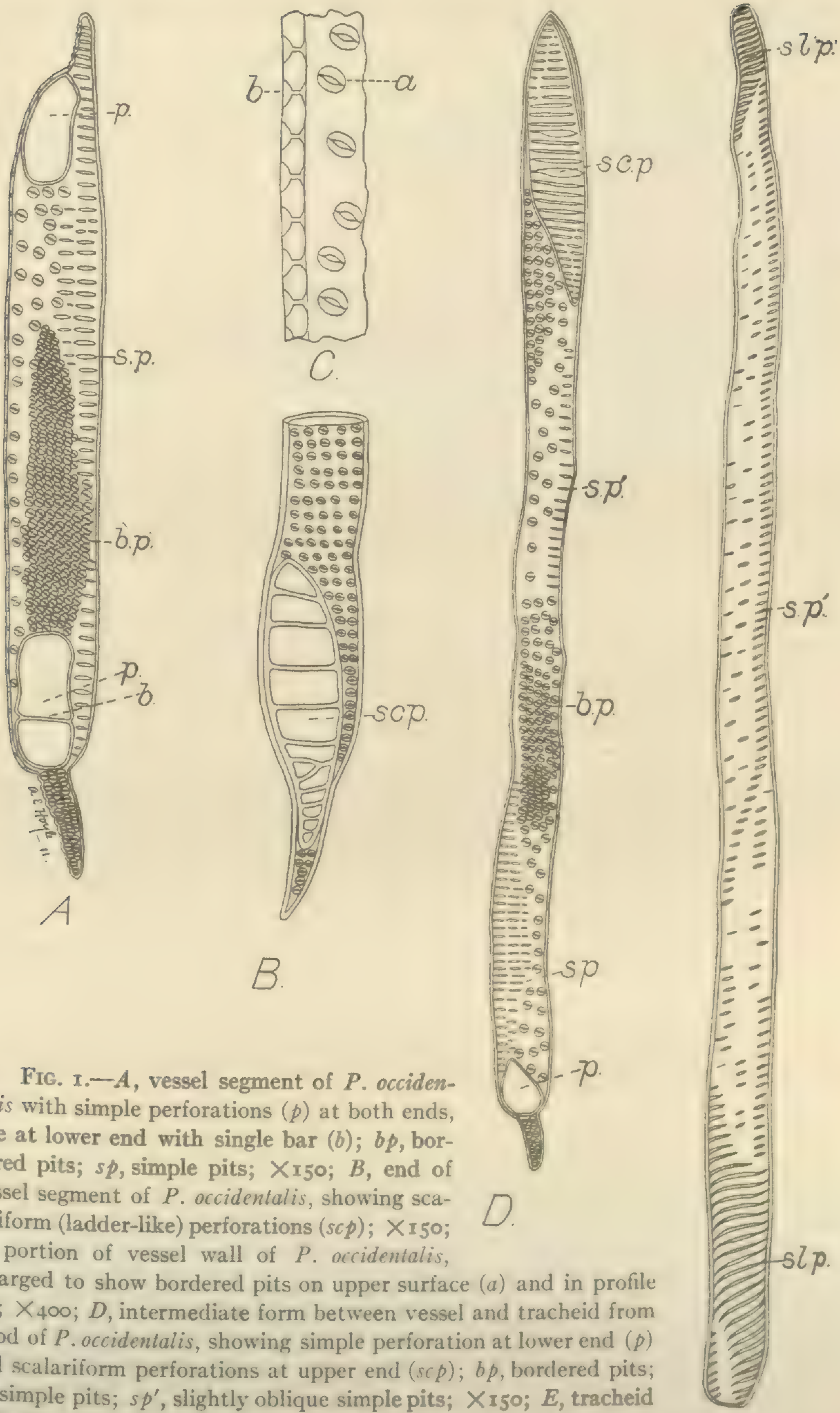

FIG. 1.—*A*, vessel segment of *P. occidentalis* with simple perforations (*p*) at both ends, one at lower end with single bar (*b*); *bp*, bordered pits; *sp*, simple pits; ×150; *B*, end of vessel segment of *P. occidentalis*, showing scalariform (ladder-like) perforations (*scp*); ×150; *C*, portion of vessel wall of *P. occidentalis*, enlarged to show bordered pits on upper surface (*a*) and in profile (*b*); ×400; *D*, intermediate form between vessel and tracheid from wood of *P. occidentalis*, showing simple perforation at lower end (*p*) and scalariform perforations at upper end (*scp*); *bp*, bordered pits; *sp*, simple pits; *sp'*, slightly oblique simple pits; ×150; *E*, tracheid of *P. Wrightii* with slitlike perforations at both ends (*slp*); *sp*, simple pits; ×150.

the "typical tracheid" or "true tracheid." This form, which occurs in the wood of practically all of the broadleaf trees, is analogous to the tracheid of the conifers. From the primitive tracheid form there seem to have developed throughout the broadleaf tree species two highly specialized forms, vessel and wood fiber. In the genus *Platanus* the general term "tracheid" must be made to include all transitional forms between the typical tracheid and the vessel on the one side, and between the typical tracheid and the wood fiber on the other side.

The typical tracheid is moderately thin-walled, has oblique simple pits, and the perforations at the ends are slitlike (fig. 1, *E*). The tracheid forms between the typical tracheid and the vessel possess, in addition to the oblique simple pits, rows of oblique bordered pits and transverse simple pits, both of which forms occur in the walls of vessels (fig. 1, *A* and *D*, *bp* and *sp*); and the perforations at the ends may be simple, either with or without bars, or scalariform, as in vessels; or the perforation may be a transitional form between the scalariform as found in vessels and the slitlike perforations found in true tracheids (fig. 1, *D*, *sp*). The tracheid forms between the typical tracheid and the wood fiber are somewhat slender, pointed at both ends, and thick-walled, and possess the vertical bordered pits of wood fibers in addition to the oblique simple pits belonging to tracheids. They often have also small transverse slits like those in the ends of true tracheids (fig. 2, *D*, *slp*). These tracheid forms (or tracheids) of sycamore wood, therefore, although extremely variable, may be defined as moderately thin-walled, elongated elements with slightly oblique elliptical or slitlike simple pits and slitlike perforations at the ends. They may also possess those pits common to either vessels or wood fibers, and the perforation at the ends may be simple, scalariform, or slitlike, these types often grading into each other.[3] The average tracheid is 1.3 mm. in length and about 0.04 mm. in diameter.

[3] A study of such transitional forms as are found in the wood of the sycamores is of great value to the student in wood structure, in that it shows the relationship of the elements to each other and assists in their classification and in the recognition of the essential features belonging to each class.

WOOD PARENCHYMA FIBERS

Wood parenchyma fibers, used for the storage of food materials, are usually less than half the length of the wood fibers, are moderately thin-walled, and composed of a number of individual cells. In sycamore woods wood parenchyma fibers occur only in the neighborhood of vessels and pith rays, from which they obtain their food supply. Each fiber consists of 1–8 oblong or cubical cells. Two forms of wood parenchyma fibers may be distinguished in sycamore wood. The fibers of the first form communicate directly with the vessels and have large transverse simple pits (fig. 2, *A*). The fibers of the second form communicate with one another and with those of the first form, but they do not communicate directly with the vessels; these have dotlike bordered pits (fig. 2, *B*).

INTERMEDIATE FIBERS

Intermediate fibers, although very similar to wood fibers, also serve for food storage. They are slightly thinner-walled and shorter than the latter and possess many small oval oblique bordered pits. They may be distinguished from the wood fibers, among which they are sparsely scattered, by the starch contained in them. They are intermediate in form and function between wood parenchyma fibers and wood fibers; hence the term "intermediate fiber."

PITH RAYS

The three species of sycamore woods may be distinguished from each other by the pith rays. The rays of common sycamore are much broader in tangential section (pl. XXXV, *pr*) than those of the other two species. They have an average width of 14 cells, and the ratio of width to height is 1:5. The rays are narrowest in the California sycamore (pl. XXXVII, *pr*); they average only 5 cells wide, and the ratio of width to height is 1:26. The rays in Arizona sycamore (pl. XXXVI, *pr*) average 8 cells wide, and the ratio of width to height is 1:12. In all species the pith rays abruptly widen in transverse section at the boundary of each annual ring of growth (pl. XXXIII, *pr*). The pith ray cells as seen in radial section are usually much longer than they are high,

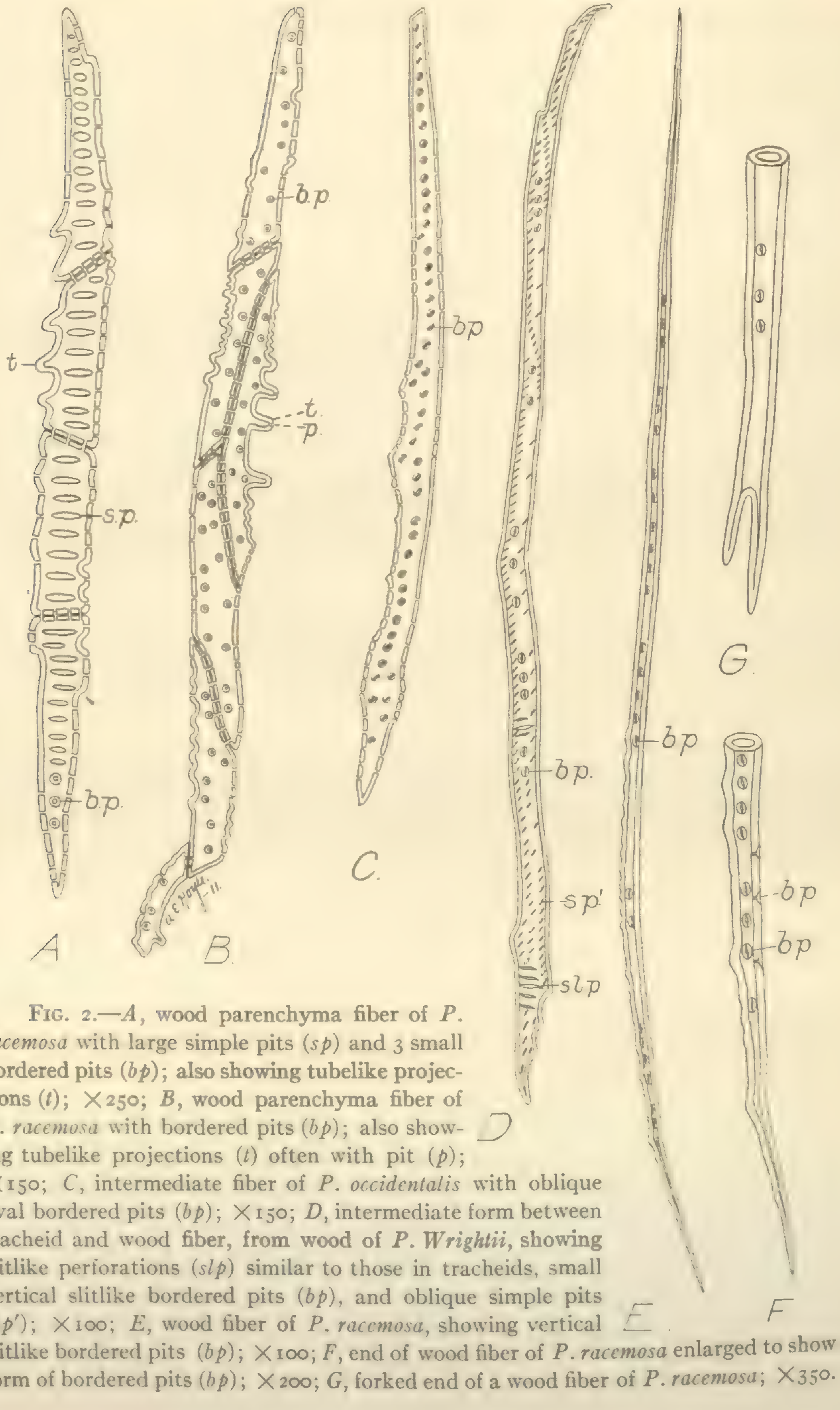

FIG. 2.—*A*, wood parenchyma fiber of *P. racemosa* with large simple pits (*sp*) and 3 small bordered pits (*bp*); also showing tubelike projections (*t*); ×250; *B*, wood parenchyma fiber of *P. racemosa* with bordered pits (*bp*); also showing tubelike projections (*t*) often with pit (*p*); ×150; *C*, intermediate fiber of *P. occidentalis* with oblique oval bordered pits (*bp*); ×150; *D*, intermediate form between tracheid and wood fiber, from wood of *P. Wrightii*, showing slitlike perforations (*slp*) similar to those in tracheids, small vertical slitlike bordered pits (*bp*), and oblique simple pits (*sp'*); ×100; *E*, wood fiber of *P. racemosa*, showing vertical slitlike bordered pits (*bp*); ×100; *F*, end of wood fiber of *P. racemosa* enlarged to show form of bordered pits (*bp*); ×200; *G*, forked end of a wood fiber of *P. racemosa*; ×350.

except toward the outer boundary of each year's growth, where they become very much shorter (pl. XXXVIII, *pr*). The cross-walls between the ray cells are sometimes vertical, but more often they are slightly oblique.

Analytical key

Pith rays 0.22–0.34 mm. wide (average 0.29 mm. or 14 cells); average height, 1.36 mm. or 50 cells; average ratio of width to height, 5.—*P. occidentalis* (pls. XXXII, XXXV, XXXVIII).

Pith rays 0.10–0.22 mm. wide (average 0.16 mm. or 8 cells); average height, 1.84 mm. or 84 cells; average ratio to height, 12.—*P. Wrightii* (pls. XXXIII, XXXVI).

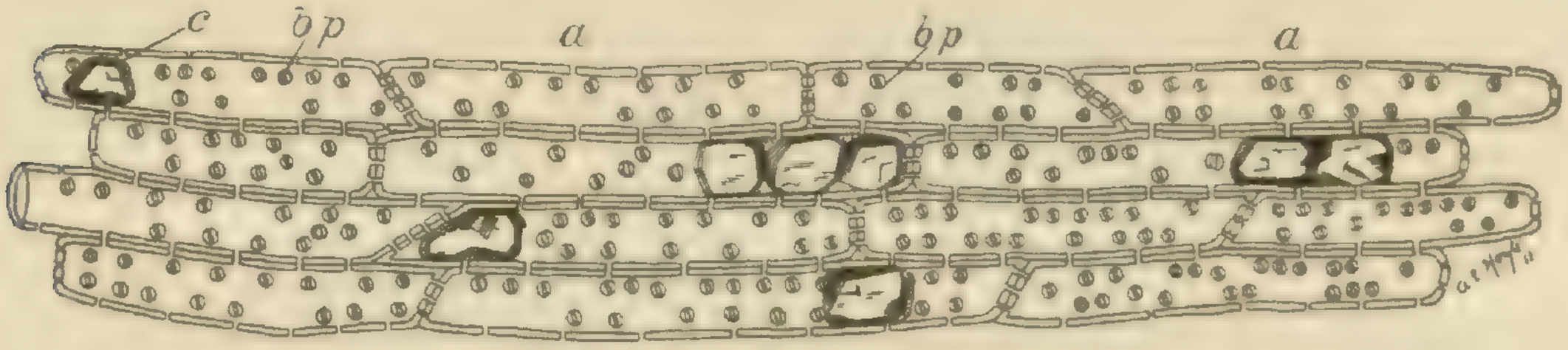

FIG. 3.—Radial view of portion of pith ray of *P. racemosa: a*, individual parenchyma cells; *bp*, bordered pits; *c*, crystal; ×200.

Pith rays 0.04–0.20 mm. wide (average 0.09 mm. or 5 cells); average height, 2.36 mm. or 107 cells; average ratio of width to height, 26.—*P. racemosa* (pls. XXXIV, XXXVII).

Individual characteristics

P. occidentalis L., common sycamore

(pls. XXXII, XXXV, XXXVIII)

Distribution.—Southeastern New Hampshire and southern Maine to northern Vermont and Lake Ontario (Don River, near north shores of the lake); west to eastern Nebraska and Kansas, and south to northern Florida, central Alabama and Mississippi, and Texas (Brazos River and thence south to Devils River).

Uses.—Common sycamore is used to a large extent for plug tobacco boxes, furniture, butchers' blocks, ox yokes, wooden bowls, and cooperage, blind wood in cabinet work, chairs, refrigerators,

parquetry, sewing machines, picture molding, saddletrees, vehicles, and bookcases. It is cut radially for veneer. This is because the "silver grain," made by the large pith rays, is very prominent, thus giving the appearance of oak.

Gross characters.—The wood is moderately hard and heavy, not strong, close-grained, very tough, usually exceedingly cross-grained, difficult to split, and not durable in contact with the soil. It is easier to split when dry, but is liable to warp in seasoning. The heartwood is a reddish brown, especially in older trees, with a decidedly reddish color in the pith rays; the sapwood is light brown, and the transition from sapwood to heartwood is quite gradual. The annual rings of growth (pl. XXXII) are less clearly defined than in the two western species. The pith rays are very conspicuous (pl. XXXII, *pr*).

Vessels (transverse section, pl. XXXII, *v*).—These occur either singly or else in irregular groups of 2–5. The last arrangement is the usual one in the early wood. At the beginning of each annual ring and immediately adjacent to the several rows of much radially flattened wood fibers which mark the end of the preceding growth layer is an interrupted row of tangentially compressed vessels (pl. XXXII, *v*) somewhat larger than those formed later. The vessels diminish slightly in diameter and in number toward the outer part of the annual ring, where they are usually isolated. They measure 0.06–0.10 mm., with an average of 0.083 mm. in diameter (table II). Vessel segments (tangential section, pl. XXXV, *v*) vary from 0.72 to 0.89 mm. in length, with an average of 0.786 mm. (table III). The vessel walls are much thinner than those of the surrounding cells. Where two segments join endwise, the opening between them is large and elliptical, or often the end walls are not completely absorbed, leaving a scalariform or ladder-like opening, with 1–25 bars like those found in the ends of the tracheids (fig. 1, *B*). These bars are much narrower than the openings or slits between them and are often branched. The oblique end of the vessel segment is often prolonged, forming a projection which overlaps the adjoining segment above and below. The vessel walls are marked by vertical and horizontal rows of numerous small, slit-like, bordered pits, which are horizontal, or often slightly oblique.

These serve as means of communication between vessels. Large transversely elongated, oval, simple pits connect the vessels with wood parenchyma fibers (fig. 1, *A*, *sp*).

Tracheids (pl. XXXII, *t*).—These are numerous and variable in form, and all gradations between vessels and wood fibers may be found. True tracheids have numerous slightly oblique, elliptical, or slitlike simple pits (fig. 1, *E*, *sp*) throughout their entire length, and at both ends there are many long slitlike openings where they overlap other tracheids above and below (fig. 1, *E*, *slp*). In addition to these pits of the true tracheids most tracheids possess rows of slitlike bordered pits and the transverse oval simple pits found in vessels (fig. 1, *D* and *A*, *sp* and *bp*); hence they somewhat closely resemble vessels. Also many of the tracheids have at one or both ends a simple perforation (fig. 1, *D*, *p*) either with or without bars, like those in vessels, in place of the slitlike openings found in true tracheids, or else the perforation at the end may be intermediate between the slitlike and scalariform types (fig. 1, *D*, *scp*). Tracheids are also found which resemble wood fibers, but these are not numerous. They possess, in addition to the oblique simple pits of tracheids, the small vertical or often slightly oblique slitlike bordered pits which characterize wood fibers (fig. 2, *D* and *E*, *bp*). These tracheids are usually more or less pointed at both ends and sometimes possess small slitlike perforations similar to those found in true tracheids (fig. 2, *D*, *slp*).

Wood fibers.—These are round, angular, or flattened in transverse section (pl. XXXII, *wf*). They are long, slender, and long-acuminate at the ends, and are marked by numerous small slitlike, obscurely bordered pits[4] (fig. 2, *E* and *F*, *bp*). The pits are vertical or oblique, often at an angle of 45°, the oblique position being greatest in fibers with wide lumina. The ends are sharply pointed and often conspicuously forked (fig. 2, *G*). They vary from 1.39 to 2.02 mm. in length, with an average of 1.63 mm. The broad thin-walled wood fibers, as already described, often show a resemblance to tracheids.

Wood parenchyma fibers.—These have acute ends, are moderately thin-walled, and are composed usually of 4–8 individual cells.

[4] The border is hardly visible where the fibers have been isolated by maceration.

Two types of wood parenchyma fibers may be distinguished in the wood of the sycamores, although these may grade somewhat into each other. The elements of one of these types are found adjacent to vessels, which they somewhat resemble and with which they communicate through horizontally elongated elliptical simple pits (fig. 2, *A*, *sp*). Small dotlike or circular bordered pits are also sometimes found in these elements which put the wood parenchyma fibers in communication with one another. The cross-walls between individual cells are usually slightly oblique and are pierced by numerous slightly bordered pits. The second type is larger, usually more tapering at the ends, and the individual cells composing it vary considerably in size and form, so that frequently one individual cell is found overlapping two other cells of the same fiber (fig. 2, *B*). The cross-walls are usually oblique, often approaching the vertical, so that the individual cells are often pointed at the end. This type is characterized by small round or dotlike, slightly bordered[5] pits (fig. 2, *B*, *bp*), which put them in communication with pith ray cells and other wood parenchyma fibers. The walls in certain places are often locally thickened.

Wood parenchyma fibers slightly separated by two contiguous vessels often connect by means of tubular outgrowths from their lateral walls (fig. 2, *A* and *B*, *t*). By means of these tubular projections, which are usually pitted at the points where they join, wood parenchyma fibers communicate with one another. Frequently these projections end blindly.

Intermediate fibers (fig. 2, *C*).—These resemble wood parenchyma fibers in the fact that their walls are irregularly thickened and that their ends are somewhat blunted. They more closely resemble the wood fibers in form, although broader and much shorter

[5] By some investigators a pit is considered bordered only when the pit canal widens out abruptly toward the outside of the cell wall, the outer portion forming an angle with the inner portion of the pit canal which opens into the lumen; where no such widening occurs the pit is simple. On this basis, however, all transitional forms between simple and bordered pits can be found in wood cells; hence the classification is merely an arbitrary one. It is thought best in the present paper to consider pits as bordered where the walls of the pit canals are not parallel and where they give the appearance of a border in longitudinal sections.

than the average wood fiber. They have numerous oval oblique bordered pits.

Pith rays (pls. XXXII, XXXV, XXXVIII, *pr*).—These are very conspicuous. They are on the average 14 cells (0.29 mm.) in width and are about 5 times as high. The pith ray cells are elliptical in the tangential section and are usually much elongated radially. The side walls are thickened and marked by many dotlike slightly bordered pits which place them in communication with the surrounding elements (fig. 3, *bp*). Crystals are very abundant in the pith ray cells.

P. Wrightii S. Wats., Arizona sycamore (pls. XXXIII, XXXVI)

Distribution.—Southwestern New Mexico and southern Arizona, Mexico (Sonora).

Uses.—The wood of Arizona sycamore is little used. This is on account of its small dimensions and the limited supply of suitable saw logs. It is very similar in its chief structural characters to the wood of California sycamore. While this wood does not occur in the market, it possesses qualities useful for the same purposes as the wood of the common sycamore, and it could be applied to these uses were the tree larger and sufficiently abundant to warrant its exploitation.

Gross characters.—The wood is somewhat lighter and softer and also less cross-grained and easier to split than that of the common sycamore. It is weak, very close-grained, and quite tough, but not very durable in contact with the soil. The sapwood is light colored or almost white, and the heartwood is light brown with a reddish tinge. The annual rings (pl. XXXIII) are clearly defined on a smooth transverse section. The pith rays are clearly visible, though not as prominent as those of the common sycamore.

Minute characters.—Vessels in transverse section (pl. XXXIII, *v*) are arranged singly or in groups, just as in the common sycamore already described. In the beginning of the early wood the vessels

form a fairly continuous row, but they gradually diminish in diameter and in number as they enter the late wood. They vary from 0.04 to 0.09 mm., with an average of 0.076 mm. in diameter (table II). The vessel segments are relatively short in this species, varying from 0.39 to 0.73 mm., with an average of 0.55 mm. in length (table III). Where two vessel segments join end to end the perforation is as in the common sycamore. *Tracheids* (pl. XXXIII, *t*) are variable in form, some closely resembling vessels and others very similar to wood fibers. *Wood fibers* (pl. XXXIII, *wf*) form the bulk of sycamore wood. The length of these elements in Arizona sycamore varies from 1.5 to 2 mm. in length, with an average of 1.7 mm. They are thick-walled and pitted as in the common sycamore. The *wood parenchyma fibers* and *intermediate fibers* of Arizona sycamore are similar in all respects to those of the other two species (fig. 2, *A*, *B*, *C*). *Pith rays* (pls. XXXIII, XXXVI, *pr*) are conspicuous; the average of the large rays is 0.16 mm. wide and about 12 times as high, and therefore much narrower and somewhat higher than in the common sycamore. The pith ray cells are round in the tangential section (pl. XXXVI, *pr*), and are usually much elongated radially.

P. racemosa Nutt., California sycamore (pls. XXXIV, XXXVII)

Distribution.—California (from the lower Sacramento River through interior valleys and coast ranges) to Lower California (San Pedro Martir Mountain).

Uses.—California sycamore wood, because of its limited supply, is used only locally and only to a small extent. It is somewhat lighter in weight and in color than the common sycamore, and is also less cross-grained and hence easier to work. Users of this wood claim that it is more durable and is also less liable to warp than the common sycamore. It should be useful for all purposes for which common sycamore is used except where great toughness is required, as in butchers' blocks, ox yokes, wooden bowls, etc. It should be found useful especially for tobacco boxes, for which the wood of the eastern sycamore is so extensively used.

Gross characters.—In general appearance the wood is similar to that of Arizona sycamore, although it is slightly lighter, softer, and more durable. Although moderately tough, somewhat cross-grained, and rather difficult to split and work, it is relatively weak. The heartwood is light brown, slightly tinged with red; the sapwood is light yellowish brown. The annual rings of growth are more or less clearly defined on a smooth transverse section (pl. XXXIV). The pith rays (pl. XXXIV, *pr*) appear as numerous conspicuous thin lines.

Minute characters.—Vessels (pl. XXXIV, *v*) are quite evenly distributed throughout the annual rings of growth and are grouped as in the other two species already described. The beginning of each annual ring is marked by a well defined row of slightly tangentially flattened pores larger than those formed later. They measure 0.06–0.09 mm. in diameter and average 0.073 mm. (table II). The average length of vessel segments is 0.677 mm., varying from 0.61 to 0.75 mm. in length (table III). Tracheids (pl. XXXIV, *t*) do not differ from those in the other two species described and show the same transitional forms to vessels and wood fibers. *Wood fibers* (pl. XXXIV, *wf*) are from 1.26 to 1.93 mm. long, with an average length of 1.55 mm. (table IV). *Wood parenchyma fibers* and *intermediate fibers* are in all respects similar to those of the other two species (fig. 2, *A*, *B*, *C*). *Pith rays* (pls. XXXIV, XXXVII, *pr*) are conspicuous in all sections. They are narrowest in this species and have an average width of 5 cells (0.09 mm.). They are on an average 26 times as high as wide, being thus much higher than in the other two species. The pith ray cells in the tangential section are round and slightly higher than broad.

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EXPLANATION OF PLATES XXXII–XXXVIII

PLATE XXXII.—Transverse section of wood of common sycamore (*P. occidentalis*), showing parts of two annual rings of growth; *ew*, early wood; *lw*, late wood; *v*, vessels; *wf*, wood fibers; *pr*, pith rays.

PLATE XXXIII.—Transverse section of wood of Arizona sycamore (*P. Wrightii*), showing parts of two annual rings of growth: *ew*, early wood; *lw*, late wood; *v*, vessels; *wf*, wood fibers; *pr*, pith rays.

PLATE XXXIV.—Transverse section of wood of California sycamore (*P. racemosa*), showing parts of two annual rings of growth: *ew*, early wood; *lw*, late wood; *v*, vessels; *wf*, wood fibers; *pr*, pith rays.

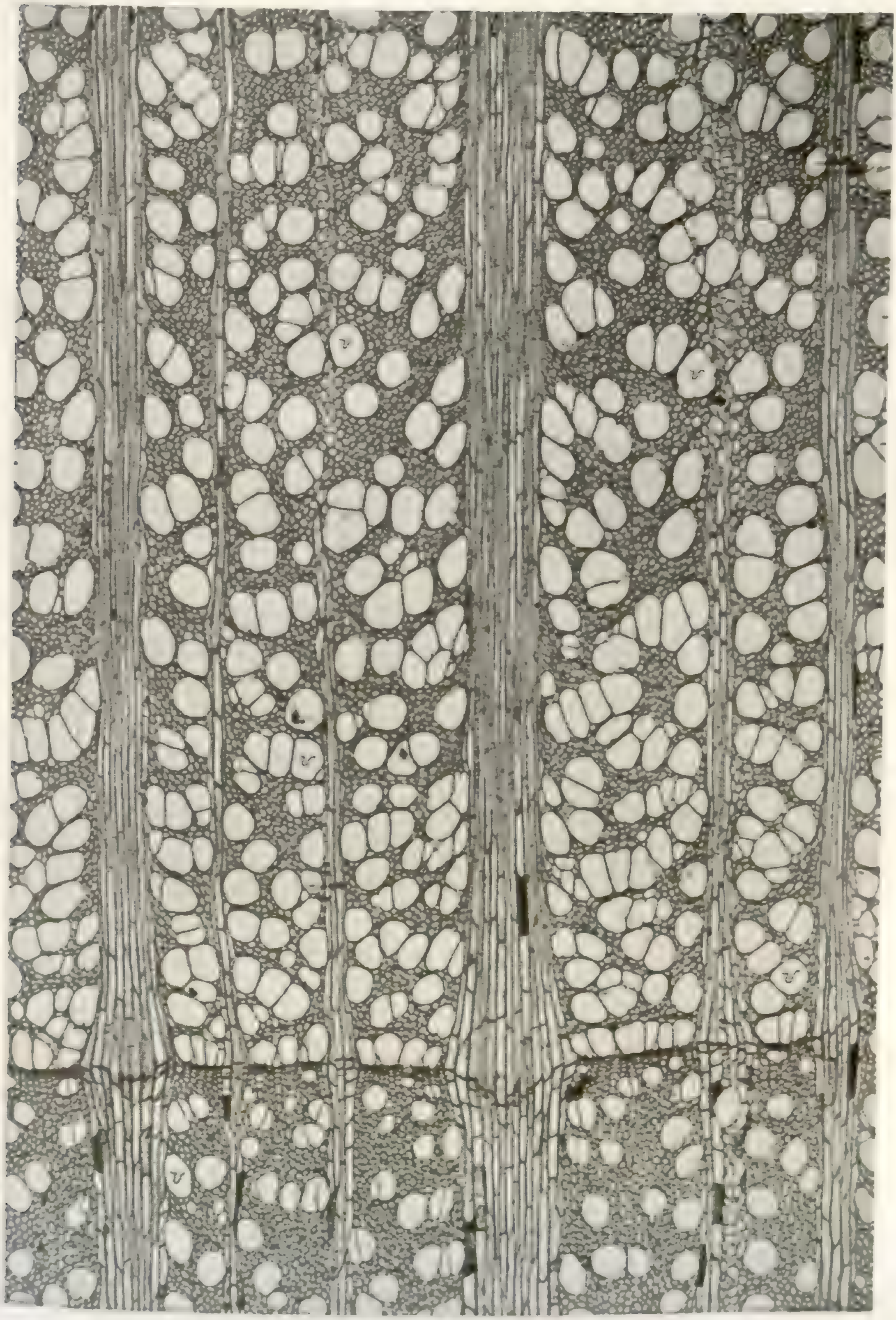
PLATE XXXV.—Tangential section of wood of common sycamore (*P. occidentalis*), showing pith rays (*pr*) in cross-section and vessels (*v*) and wood fibers (*wf*) in longitudinal section.

PLATE XXXVI.—Tangential section of wood of Arizona sycamore (*P. Wrightii*): *v*, vessels; *wf*, wood fibers; *pr*, pith rays.

PLATE XXXVII.—Tangential section of wood of California sycamore (*P. racemosa*): *v*, vessels; *wf*, wood fibers; *pr*, pith rays.

PLATE XXXVIII.—Radial section of wood of common sycamore (*P. occidentalis*): *v*, vessels; *wf*, wood fibers; *pr*, pith rays.

BRUSH on SYCAMORE WOODS



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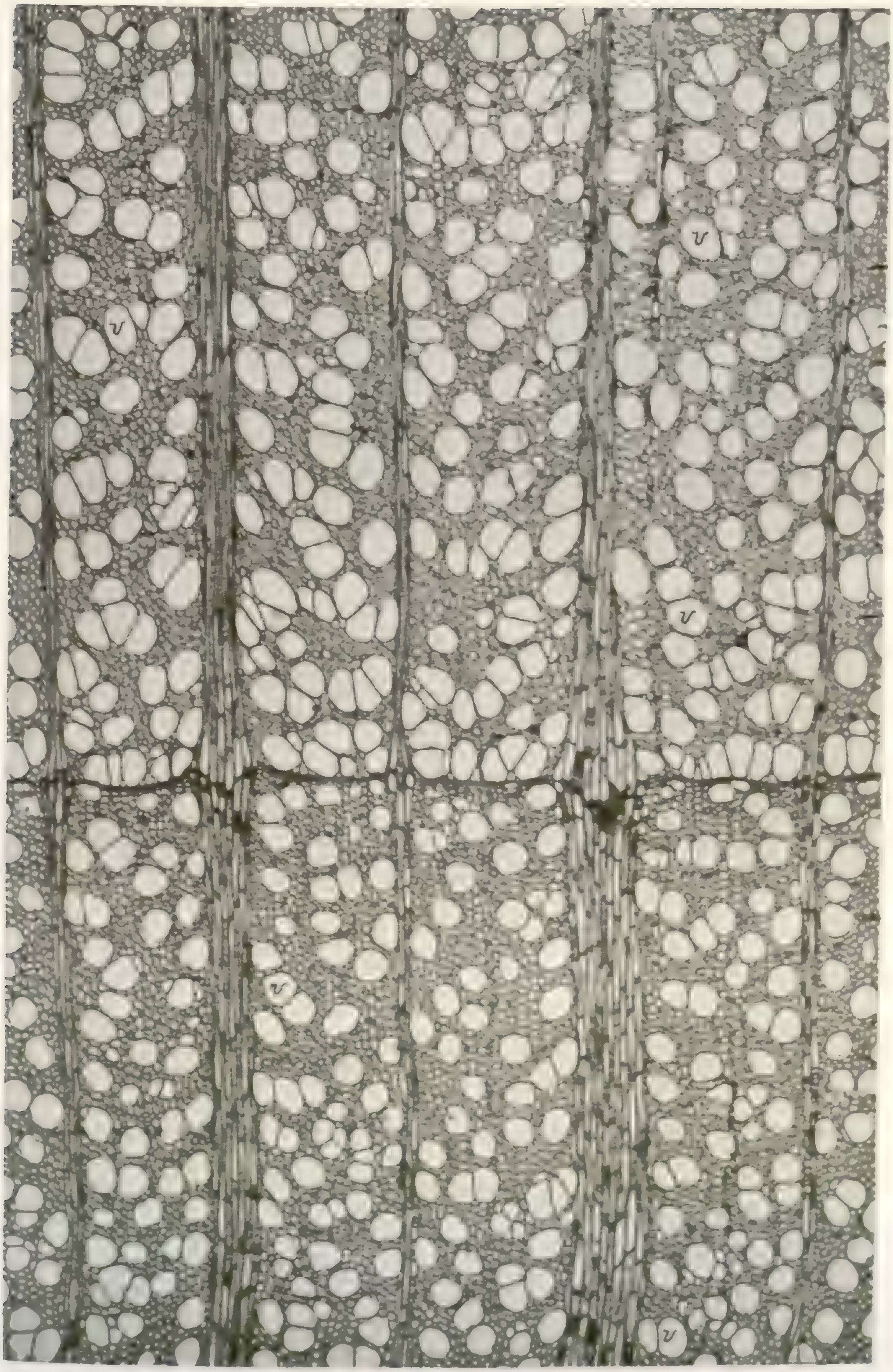

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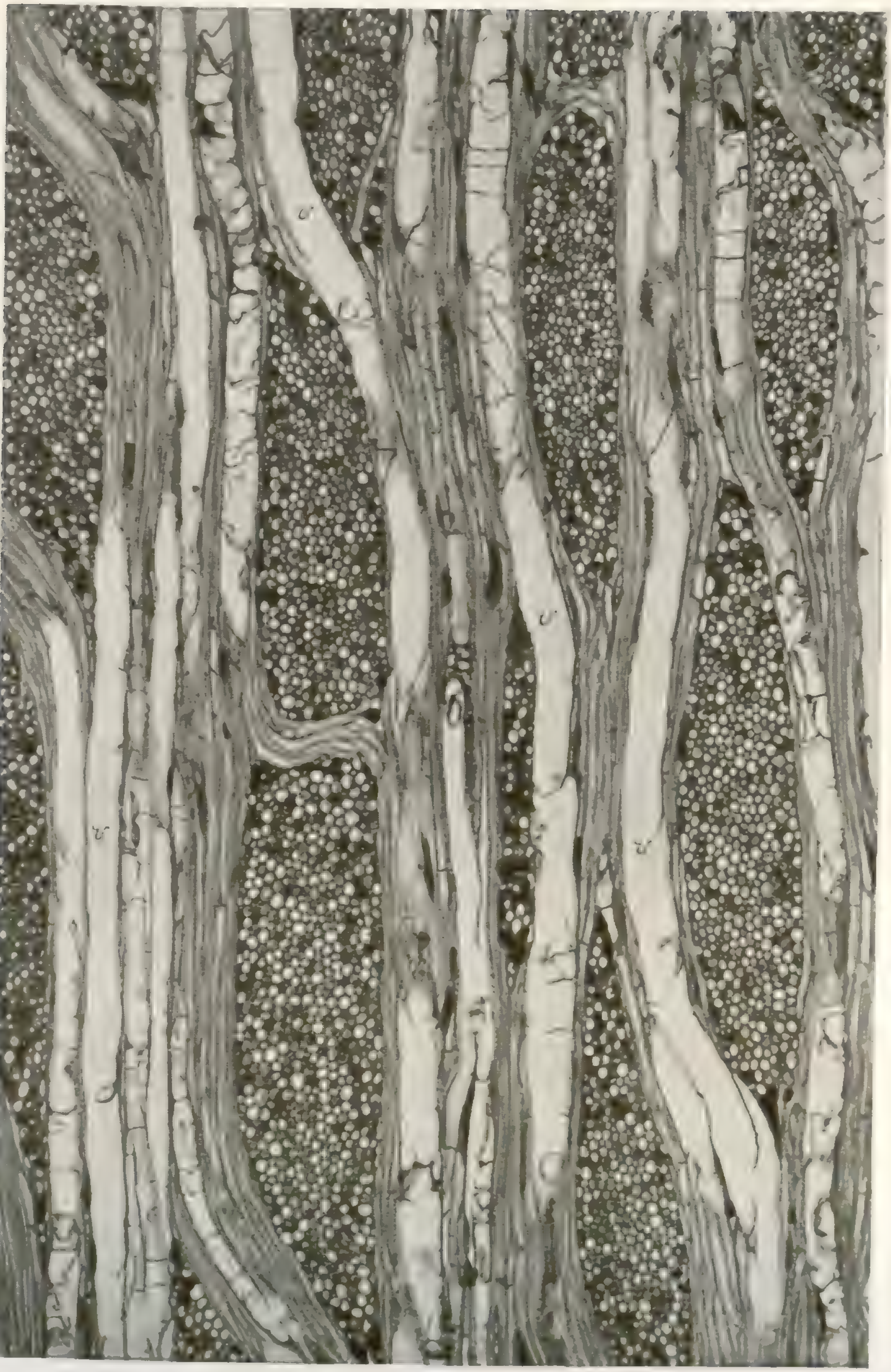

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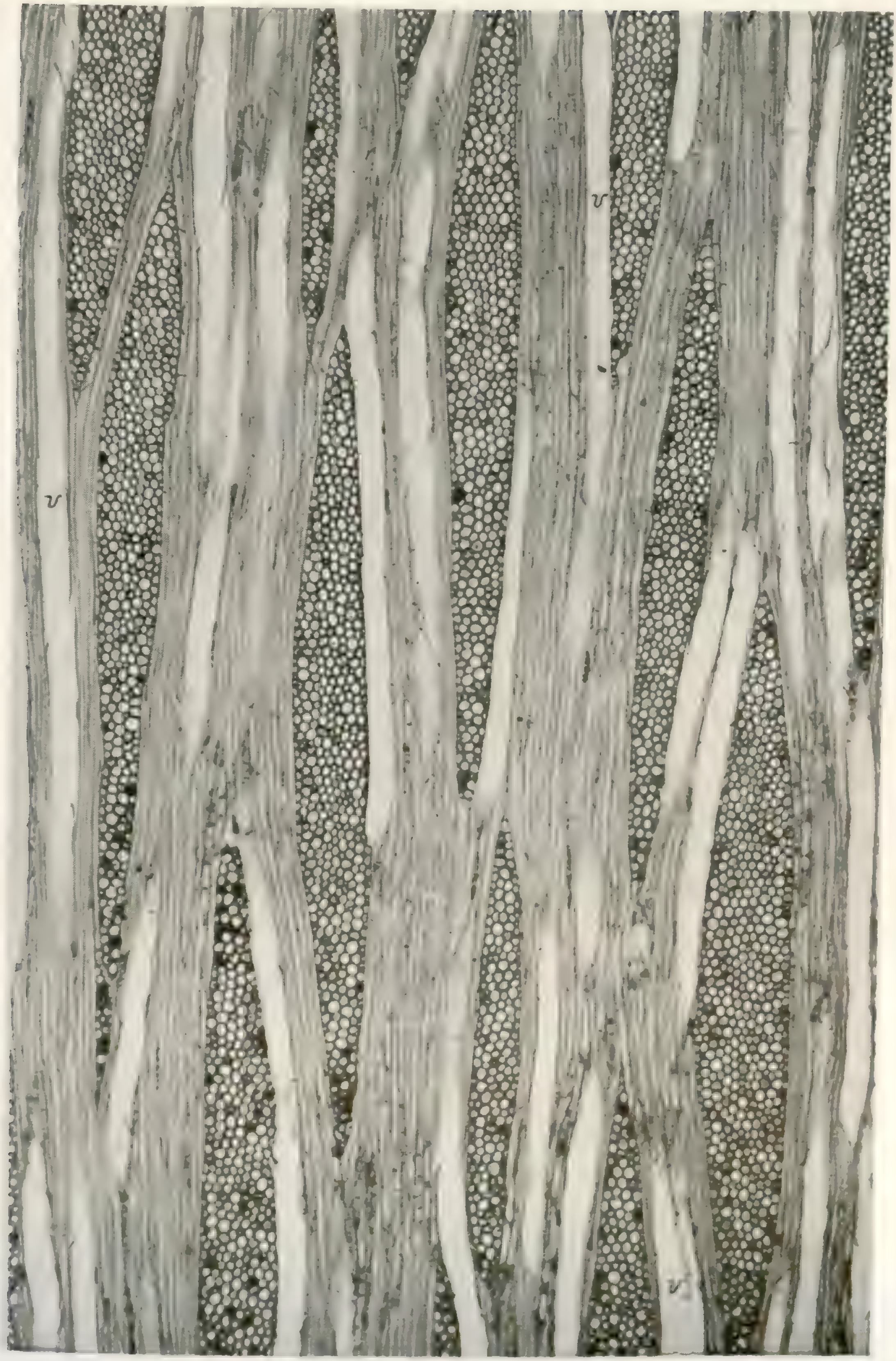

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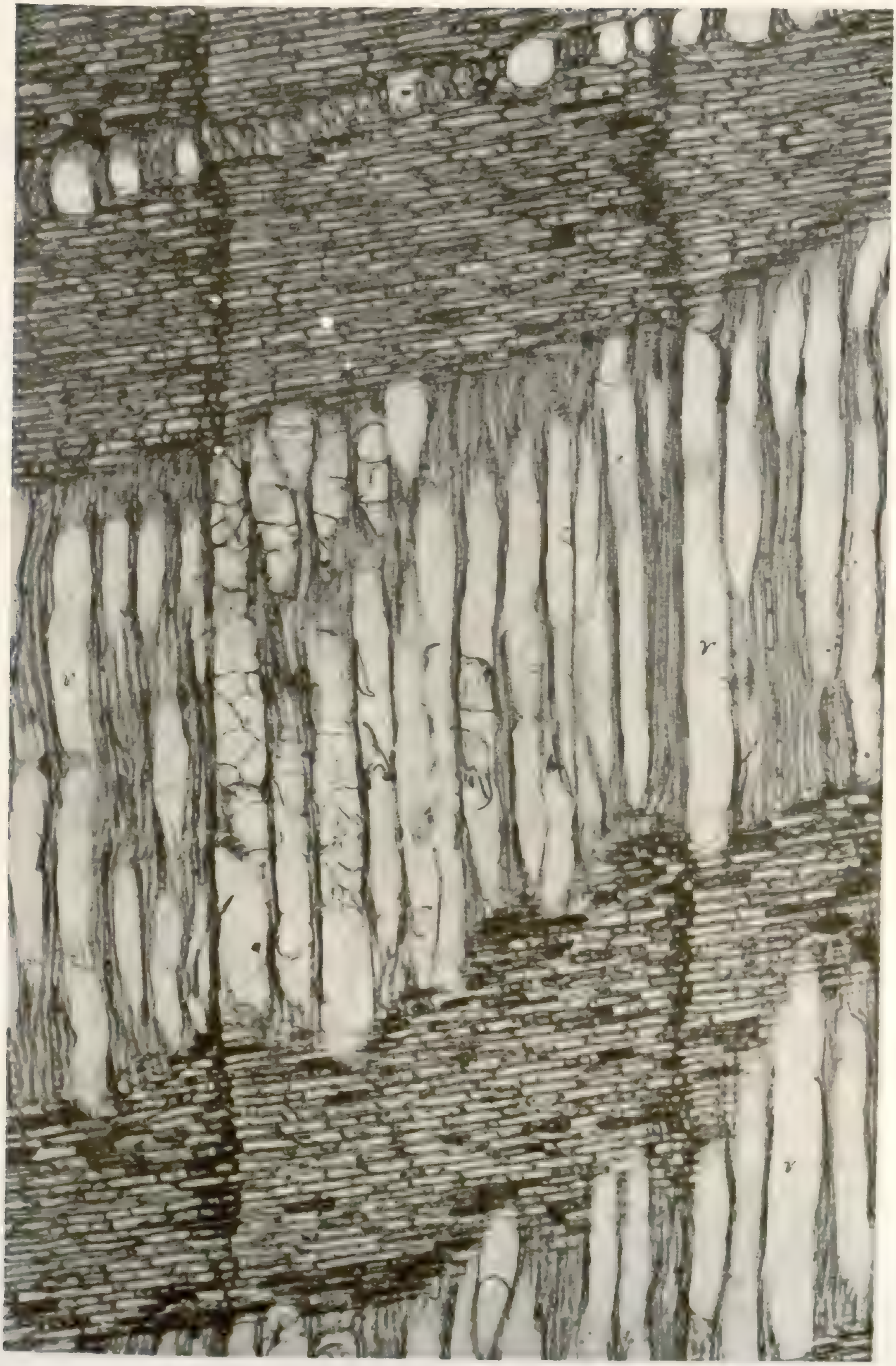


BRUSH on SYCAMORE WOODS

AGENCY OF FIRE IN PROPAGATION OF LONGLEAF PINES

E. F. Andrews

(WITH FIVE FIGURES)

The important part played by forest fires in the life history of the longleaf pine has been recognized by a number of recent writers, and Harper[1] even goes so far as to say "that if it were possible to prevent forest fires absolutely the longleaf pine . . . . would soon become extinct." The connection between the periodic recurrence of these catastrophes and the success of the pine seedlings in competing for possession of the soil was pointed out by Mrs. Ellen Call Long, of Tallahassee, more than 25 years ago, but the suggestion appears on the face of it so at variance with universal experience as to give little occasion for surprise that it should have been received with incredulity, or at best with indifference, by those unacquainted with the adaptive provisions of the species and the conditions prevailing in its habitat.

The writer has recently been favored with exceptional opportunities for investigating this subject by means of an experiment carried out by nature herself, in the native home of the longleafs, with all the exactness of detail that could be expected in a well ordered laboratory. Even that refined test of scientific accuracy, a control experiment, was provided by a neighboring group of the same species that was not exposed to fire on the occasion referred to. The scene of this spontaneous demonstration lies on the northern slope of Lavender Mountain, in Floyd County, Georgia, a ridge of the Southern Appalachians which is certainly very near, if not actually itself, the extreme inland and upland limit of the longleaf pines as they occur at present. The crest of the ridge, according to the United States Geological Survey, attains a maximum height of 1695 ft. above sea level, and extends for 12 miles or more in an approximately east and west direction. It is divided

[1] Economic Botany of Alabama, Part 1, p. 26.

transversely by three deep depressions, or gaps, through which traffic is carried on, and the intervals between the gaps are subdivided by numerous ravines into more or less widely separated spurs and knobs. The southern slopes are covered with the remains of great forests of this valuable timber, interspersed with various hardwood trees and with shortleaf pines (*P. virginiana* and *P. echinata*).

FIG. 1.—Young longleaf pines reforesting mountain side after removal of ripe timber

They have repeatedly been cut for lumber and burned over by "ground fires" started in spring by farmers to provide a free range for their cattle, but the longleafs continue to reproduce themselves with a pertinacity which, if not too diligently thwarted by the blundering incompetence of county officials and the short-sighted greed of ignorant timber cutters, will in the course of a generation or two repopulate the southern mountain slopes with a new forest growth sprung from the old stock (fig. 1).

While there are traditions of the former presence of this species on the northern side of the mountain, the only traces of them that I have been able to find there consist of two small, isolated groups which furnished the apparatus for nature's instructive experiment alluded to. They are situated on opposite sides of a deep ravine which starts near the top of the mountain, at Fouché Gap (the westernmost of the three passes), and descends in a gradually widening rift to the bottom. The larger and more important of these groups occupies a portion of a steep incline between the crest of the ridge and a now abandoned road that winds along the eastern edge of the ravine. It numbered only five individuals, so far as could be seen when I first took note of them, in the summer of 1913. Of these, the rugged patriarch shown in the center of fig. 2, together with two smaller specimens in the background, one of them a mere sapling, were the only members of the colony conspicuous enough to attract the attention of any but a particularly interested observer. The other two were seedlings not over 4–5 dm. in height, and at this stage of development, when the needles are the only part above ground, so like the coarse grasses around them that even an expert, unless keenly on the lookout, would be liable to pass them by unnoticed (fig. 3).

This group of five individuals was scattered over an area of half an acre, more or less, on the edge of an open copsewood which has repeatedly been cut for timber and cleared of undergrowth by minor forest fires. The rest of the declivity, from the gap to the crest of the ridge, had been cleared several years before for cotton planting, but after a short trial was abandoned as too rugged for cultivation. It was at this time (July 1913) neck deep in weeds, mixed with a scrub growth of brush and brambles; and not being in quest of the zoological specimens likely to abound in such places, I did not explore this jungle until two years later, after one of the periodical spring fires had cleared the ground.

The second group, which served as the "control," is situated on the farther side of a low spur or knoll, separated from the neighboring colony by the intervening ravine and the wooded crown of the knoll. It included, when first observed, four individuals, three of which were adults of full cone-bearing age, the

largest one measuring 2 m. in girth. The offspring of these was limited to one solitary seedling, a disproportion the significance of which will be apparent later, when compared with the progeny of the "patriarch" on the other side of the gorge. The soil in both situations is the same, a hard, dry, rocky clay, with a characteristic

FIG. 2.—In foreground, small portion of old clearing as it appeared after fire, with "patriarch" on border between it and copsewood; tall *Pinus echinata* dimly outlined at extreme left stands near brow of opposite slope of ravine; beyond is knoll on farther side of which "control" group is situated.

ground cover of *Pteris aquilina*, *Tephrosia virginica*, and a number of coarse grasses that have a strikingly familiar aspect to one acquainted with the vegetation of the great pine region of the South Atlantic coastal plain. The typical wire grass (*Aristida stricta*) of

the southern forests is here replaced by a correspondingly arid growth of "old field broom" (principally *Andropogon furcatus*, *A. virginicus*, and *A. scoparius*), with a few sedges (*Scleria triglomerata*, *Cyperus retrofractus*, etc.) intermixed. In fact, the only difference in the environment of the two groups is the isolated position of the knoll,

FIG. 3.—Large clump of spearlike leaves near upper lefthand corner is longleaf seedling; others are grasses that have sprung up since fire; skeleton plant on right and white patches in background are hardwood seedlings and bushes killed by fire that left pine seedling unharmed.

the top of which is protected by an encircling turnpike road and by the wooded slopes of two deep ravines, watered by mountain springs and clothed with a heavy growth of broad-leaved trees, conditions which oppose an effective barrier against the spread of fire.

It was not until April 1915 that I made another visit to these straggling longleaf outposts, which had interested me at first merely as landmarks of what seemed to be the *ultima Thule* of their advance in this direction. But a great surprise awaited me. The region around the gap had recently been burned over, and amid the wreckage of skeleton limbs and blackened stubs to which the weedy jungle in the old clearing was now reduced, there appeared a thriving colony of 33 young longleafs, ranging from a few decimeters to a meter or more in height. This new growth was confined mainly to the old clearing, although the "patriarch," whose progeny it presumably is, stands squarely on the border line between the old cotton field and the copsewood, and had no doubt distributed his favors impartially to both. But the absence of trees in the clearing would naturally facilitate the scattering of seeds in that direction, and during the first year or two, before the weeds and brush began to crowd them out, they would germinate freely in the open ground. I had simply overlooked them on my former visit, for the reason that they were hidden in the jungle, where, after making a successful start in life during the palmy days before their little Belgium was overrun by the horde of weedy invaders, they were at last overpowered by numbers and buried out of sight. Deprived of the sunshine so necessary to this sun-loving race, all save the oldest and strongest among them must have perished but for the timely intervention of their powerful ally, the fire, which swept away all rivals and left the young longleafs in undisputed possession of the soil. That such was the case, we have their own direct testimony, for every one of them bore unmistakable marks of fire. Some were so scorched and blackened that any one unacquainted with the habit of the species would unhesitatingly have pronounced them dead. An examination, however, of a number of the worst injured plants showed that in not a single instance had the growing point been killed, or even seriously damaged.

On the other side of the ravine conditions were unchanged except that a new road had been cut around the knoll since my former visit, almost completely encircling it, and one of the adult pines that stood in their way had been felled by the road builders.

The fire had not spread in this direction, and I had some difficulty in finding again, among the coarse grasses which these nurslings so closely resemble, the solitary seedling upon which the future hopes of the colony depend. A careful search among the undergrowth failed to bring to light any further additions to this decadent family, and, as matters now stand, it looks as though the last remnants of the longleaf forest that once clothed the knoll were doomed to early extinction.[2]

It would, of course, be rash to attribute this result solely to the absence of fires. Various other factors may intervene, among which must be reckoned the infrequency of seeding that characterizes this species, a full crop being produced only at intervals of four or five years. If a forest fire should occur during one of these "lean" periods, it would have comparatively little effect, since there would be few seedlings to take advantage of the opportunity offered, while one closely preceding a season of abundance would prepare the way for a proportionate increase in the longleaf population.

Another fact to be considered is that the early growth of the longleaf seedling is very slow. The main energy of the plant during the first year or two is expended in developing the long taproot which enables it to cope successfully with the poverty of its habitat by making the most of the meager resources of the soil, and later provides a safe anchorage for the towering shaft of the adult tree. The young specimen shown in fig. 4, and scarcely distinguishable as yet from a clump of grass, is not less than two years old, and may be more. But while giving due weight to these considerations, I think that after we have studied the effects of fire a little more closely in those cases where its agency is too obvious to be doubted, we cannot deny that it is, and has been in the past, an important factor in the propagation and distribution of the longleaf pines.

In July and August of the same year (1915) I made a longer stay on the mountain, during which time I was able to continue my observations on the pines to better advantage. In the lower

[2] Later observations (September 1917) show a flourishing group of 66 saplings and seedlings in the first colony; while the lower one on the knoll has been reduced to 2 individuals by the loss of the seedling and one of the adult trees.

group, on the knoll, there was little of interest to record, everything remaining very much as when I last saw it. On the upper slope, however, matters were very different, and a more exact count brought the census of the new generation up to 40. Of this number, all of those within the old clearing must have germinated during the 7 or 8 years since the cultivation of this part of the land

FIG. 4.—Thrifty longleaf seedling that has established itself successfully on stratum of almost solid rock, made possible by long taproot reaching far down into subsoil.

was abandoned, for they would assuredly have been weeded out had any of them dared to show their heads above ground where "cotton was king." To estimate the ages of different individuals with accuracy, however, is not easy, on account of the great irregularity in the rate of growth. While very slow during the first 2 or 3 years, as already pointed out, it becomes proportionately rapid after the critical period of "infant mortality" is past. The growth for the year 1915, up to the first of August, on two saplings of 2.75 and 2 m. in height respectively, was found by measurement

to be approximately 8 and 7.5 dm., while seedlings 12–18 cm. high showed a gain of only 2–4 cm. for the same period.

These figures show that the young longleaf, after attaining adolescence, is fully capable of holding its own in the competitive strife of the plant world. The chief danger to the species in this unceasing contest is in the risk that the seedling, during its long period of infancy, may be starved and crowded to death by the rapidly advancing host of weeds and bushes that outstrip it in the battle for food and sunlight. Their only safeguard against these enemies is, as we have seen, the forest fire.

This naturally brings up the question, how does it happen that the young pines themselves are not killed by the heat which destroys their hardier competitors? The answer is before our eyes. The great rosettes of bristling needles, which give to the longleaf pine its venerable aspect, are not the mere decorative emblems of ancient descent that they seem. They are fulfilling the important function of a defensive armor against the most destructive enemy (after man) that the plant population of the world is exposed to. The young of most species quickly succumb at the first onset of even an ordinary ground fire; but the longleaf pine seedling has its growing point closely enveloped in a crown of spearlike needles, as shown in fig. 4, before the stem begins to rise above the ground. These may be anywhere from 20 to 40 cm. long, including the sheaths, which average about 3–4 cm. When fresh they ignite so slowly as to be practically incombustible. Strictly speaking, they can hardly be said to ignite at all, but are bitten off and consumed where the fire comes in contact with them. Moreover, the application of heat causes a violent sizzling and contortion of the parts affected, accompanied by a series of small explosions which are sometimes capable of extinguishing a match; and I have even known them, on one occasion, to put out the flame of a candle. At another time, I was trying to ignite a fresh "pinetop" (as these tufts are called in our Georgia vernacular) by the flame of a kerosene lamp, when it fumed and sputtered and caused such a commotion in the burning wick that I cut short the experiment for fear of exploding the lamp and transferred my operations to the kitchen. There was a slow wood fire in the

stove, into which I thrust the pinetop, and awaited results, watch in hand. When I removed the stub at the end of 4 minutes, the needles had all been consumed, but the sheaths, especially those of the vigorous young fascicles crowded around the growing point, remained for the most part intact. The bud itself, though considerably scorched and blackened externally, appeared, like the stem, not to have suffered beyond the possibility of recovery, though this point, as the final result will show, was open to doubt.

It may be explained here that in excursions through the mountains it is desirable to avoid all unnecessary encumbrances in the way of luggage, and, as the conditions of life are very primitive in the regions of greatest interest to the botanist, one often has to resort to homely makeshifts when supplementing observation by experiment. It is surprising, however, what interesting results may sometimes be obtained by very simple means when one is determined to get to the bottom of a thing.

To complete the experiment, I next placed a couple of fresh pinetops in an upright position over a brisk blaze of chips and twigs out of doors, so as to approximate, as closely as possible, the normal conditions of an ordinary brush fire. After 8.5 minutes, when the flame had subsided and the needles were all burned away, down to their sheathed bases, I placed the stubs in water, together with the one that had been subjected to the ordeal of the kitchen stove on the day before. At the end of 12 days, when my stay on the mountain came to an end, the latter was found to have sustained internal injuries which left it in all probability beyond recovery. The other two came out of the fiery ordeal, if not altogether unscathed, yet with an appearance of vitality sufficiently unimpaired to warrant the presumption that had they remained attached to the living stem, like their kindred in nature's outdoor experiment, they would, like them, quickly recover from the effects of the fire.

The effectiveness of this provision for the safety of posterity is further assured by the tendency of the needles to persist on the stem of the young shoot for several years, until the more delicate parts are lifted beyond the reach of danger. As the growth of the sapling progresses, and the increasing thickness of the bark provides for the protection of the stem, the needles become massed

around the growing axes at the end of the branches, where they form the tassel-like clusters or "pinetops" which are such a striking characteristic of the longleaf pines (fig. 5). Under the influence of light the lateral stems supporting these tassels tend to curve upward. This upright position has the advantage that the fire, which

FIG. 5.—Young longleaf pine with stem surrounded by bristling *chevaux-de-frise* of needles, growth of several successive years.

ordinarily makes its attack from below, has to cut its way through the entire phalanx of protecting needles before it can reach the growing point. If the rosettes were drooping as in the winter condition of the white pine, they would, instead of protecting the buds, act as refractors to converge the heat upon them.

With such efficient fire protection it can easily be seen why the longleaf seedling is able to withstand a degree of heat that would be fatal to older and in other respects hardier plants. The same facts also explain why, in a state of nature, these trees tend either to congregate in pure forests over large areas or to become extinct if exposed to unrestricted competition with hardwoods. In the latter case the older conifers may hold their own for a time, but as these die out from superannuation or other causes, the new generation that should replace them, unable to develop in the shade, and cut off from the sunlight by the broad leaves of the hardwoods, fails to reach maturity and the race in time becomes extinct. On the other hand, when forest fires, especially of the minor type known as "ground fires" and "brush fires," occur at not too frequent intervals, the immunity of the pines enables them to take the lead in the work of reforestation, and through the gradual elimination of their rivals to become finally the sole possessors of the soil.

ROME, GA.

PERMEABILITY OF THE CELL WALLS OF ALLIUM

S. C. Brooks

Many investigators have reported that the tissues of higher plants are almost if not quite impermeable to inorganic salts. They have usually attributed this phenomenon to the impermeability of the protoplasm to the salts used. It is quite probable, however, that the cell walls themselves may exert an important influence on the permeability of tissues. It is of interest, therefore, to point out a striking example of the impermeability of the cell wall, which was found when it was attempted to investigate, by the diffusion method recently described by the writer,[1] the permeability of epidermis from the inner surface of bulb scales of the onion. The principle of the experiment and the apparatus used were the same as in the writer's experiments on *Laminaria*, as recorded in the paper cited. Certain modifications were necessary, however.

In order to avoid injury due to drying out of the epidermis (which consists of a single layer of cells), it was necessary to reduce as much as possible the time intervening between the act of stripping the epidermis from the scale and that of filling the cells with solutions. The whole operation usually occupied about 30 seconds, a time which caused no observable injury to the cells.

Dead material was prepared by exposing freshly removed sheets of tissue to chloroform vapor for a period of one hour, then immediately immersing them in a large volume of distilled water, which was several times renewed. After 15 days in distilled water the dead tissue was used in the usual manner.

The salt solutions used in the lower cells were always 0.05 M, a concentration hypotonic to the living cells of the onion epidermis. In the upper cells there was placed distilled water having a specific conductivity of about 2×10^{-6} mhos. Extreme precautions were used to prevent access of dust, acid vapors, or any other soluble material to the distilled water in the upper cells. In all the

[1] Brooks, S. C., A new method of studying permeability. Bot. Gaz. 64:306–317. *figs. 2.* 1917.

experiments on this tissue the distilled water was obtained by distillation from an apparatus made entirely of glass, and which had been in constant operation for several weeks prior to the collection of the sample here used.[2] All the kations were used in the form of chlorides, thus making it possible to determine their concentration in the upper cell by two entirely independent methods. The conductance of known concentrations from 10^{-7} M to 10^{-3} M of the salts used was determined and a curve plotted showing for each salt the concentrations corresponding to any given conductance. The concentration of a given salt diffusing into the distilled water in the upper cell was then ascertained by comparison of the conductance of the solution in the upper cell with the curve for the corresponding salt. In addition, the chlorides in the upper cell were determined nephelometrically by the method of RICHARDS and WELLS.[3]

In neither living nor dead tissues could the presence of chlorides in the upper cell in excess of 3×10^{-5} M be detected nephelometrically, even during experiments whose duration exceeded 24 hours. The changes in conductivity were also such as would indicate a negligible increase in the concentration. It seems therefore that little or no salt can pass through the epidermis.

Experiments were then tried to determine the permeability of the tissue to dyes. The diffusion of Bordeaux red through the diaphragm from an 0.1 per cent aqueous solution in the lower cell into distilled water in the upper during 96 hours was insufficient to cause any visible change in the color of the distilled water. A similar experiment, in which the lower cell contained a 1 per cent aqueous solution of eosin (Merck's eosin bluish), was continued for 7 days; at the end of that time the distilled water in the upper cell could not be distinguished in color from fresh distilled water, even by the use of a colorimeter.

The experiments on dyes (as well as those on acids and alkalies, subsequently described) were performed on dead tissue.

[2] Water distilled from glass becomes better the longer distillation is continued, since the constant exposure to steam and hot water soon removes the more soluble constituents of the glass. Water such as that here used may be regarded as having no appreciable toxicity.

[3] RICHARDS, T. W., and WELLS, R. C., The nephelometer, an instrument for detecting and measuring opalescent precipitates. Amer. Chem. Jour. 31:235. 1904.

In the use of indicators we possess an extremely sensitive and reliable means of demonstrating the presence of small amounts of free acid or alkali in a solution. It would be possible therefore to detect the diffusion through the diaphragm of tissue of small amounts of hydrochloric acid or sodium hydroxide by adding a small amount of a suitable indicator to the distilled water in the upper cell of the apparatus. In the lower cells 0.1 M solutions of the acid and alkali were used.

A period of 43 hours was insufficient to allow the passage of an amount of sodium hydroxide great enough to cause any change in the color of the distilled water containing about 0.01 per cent of phenolphthalein, as determined by comparison in a colorimeter with fresh distilled water. The change of hydroxyl-ion concentration necessary to cause the first visible change in the color of the phenolphthalein would be that from 1×10^{-9} M to 1×10^{-5} M.

The turning point of Congo red lies at a hydrogen-ion concentration of 1×10^{-4} M. An increase of less than 1×10^{-4} M in the hydrogen-ion concentration of distilled water containing Congo red will then cause the appearance of the blue coloration in the indicator. Experiments were conducted in which the lower cells were filled with 0.1 M hydrochloric acid, and the upper cells with distilled water containing barely sufficient Congo red to cause a distinct red coloration; these showed that a period of 3–5 hours was sufficient to cause the color change in the indicator. Control experiments in which the lower cell was filled with pure distilled water showed no color change in the upper cells during 19 hours.

In order to eliminate the possibility that the permeability to hydrogen ions was the result of the action of the 0.1 M hydrochloric acid on the tissue, several of the cells in which there had been a diffusion of acid were simply rinsed out thoroughly, and the lower cell finally filled (after preliminary rinsing with the solution) with 0.1 M sodium hydroxide. The upper cell was filled with distilled water containing a slight amount of phenolphthalein. There was no color change in the distilled water up to the end of the experiment, a period of 3 days.

The inner epidermis of onion bulb scales, at least when its cells are dead, is therefore but slightly permeable to hydrochloric acid, and not perceptibly so to any other of the substances tried. These

included sodium, calcium, and aluminium chlorides, Bordeaux red, eosin, and sodium hydroxide.

This extraordinary impermeability is confined to the exterior cell walls of the epidermis, as will be seen by the following simple experiment. A sheet of epidermis stripped from the scale and mounted in water on an ordinary microscope slide, then irrigated with a 0.4 M sodium chloride solution, was strongly plasmolyzed within 30 seconds. In order that plasmolysis should occur, it was necessary that the plasmolyzing solute should pass into the space between the cell wall and the retracted protoplast. Some part of the cell wall is therefore freely permeable to sodium chloride.

Pieces of the scale, about 2 cm. square, with the epidermis still in place, were then placed in a 0.4 M sodium chloride solution. At intervals up to 30 minutes pieces were withdrawn, the surface dried with filter paper, and a small piece of epidermis from near the center of the piece of scale removed. These were placed between a microscope slide and cover slip, no water being added, and in all cases their cells were found to be wholly normal in appearance; but a few seconds' irrigation with an 0.4 M. sodium chloride solution now sufficed to cause violent plasmolysis. These experiments show that the exterior walls of the epidermal cells form a continuous layer highly impermeable to most substances and comparable to certain seed coats as described by previous investigators.[4]

Summary

1. The exterior cell wall of the epidermis from the inner surface of onion bulb scales is slightly permeable to hydrochloric acid, while it is practically impermeable to various salts, dyes, and to sodium hydroxide.

2. It is necessary to consider the influence of impermeable cell walls in interpreting experiments on the permeability of plant tissues.

LABORATORY OF PLANT PHYSIOLOGY
HARVARD UNIVERSITY

[4] Cf. BROWN, A., The selective permeability of the coverings of the seeds of *Hordeum vulgare*. Proc. Roy. Soc. London, B **81**:82. 1909; SCHROEDER, H., Über die selektive permeable Hülle des Weizenkornes. Flora **102**:186. 1911; SHULL, C. A., Semipermeability of seed coats. BOT. GAZ. **56**:169–199. 1913.

BRIEFER ARTICLES

PYRENOTHRIX NIGRA, GEN. ET SP. NOV.

(WITH FOUR FIGURES)

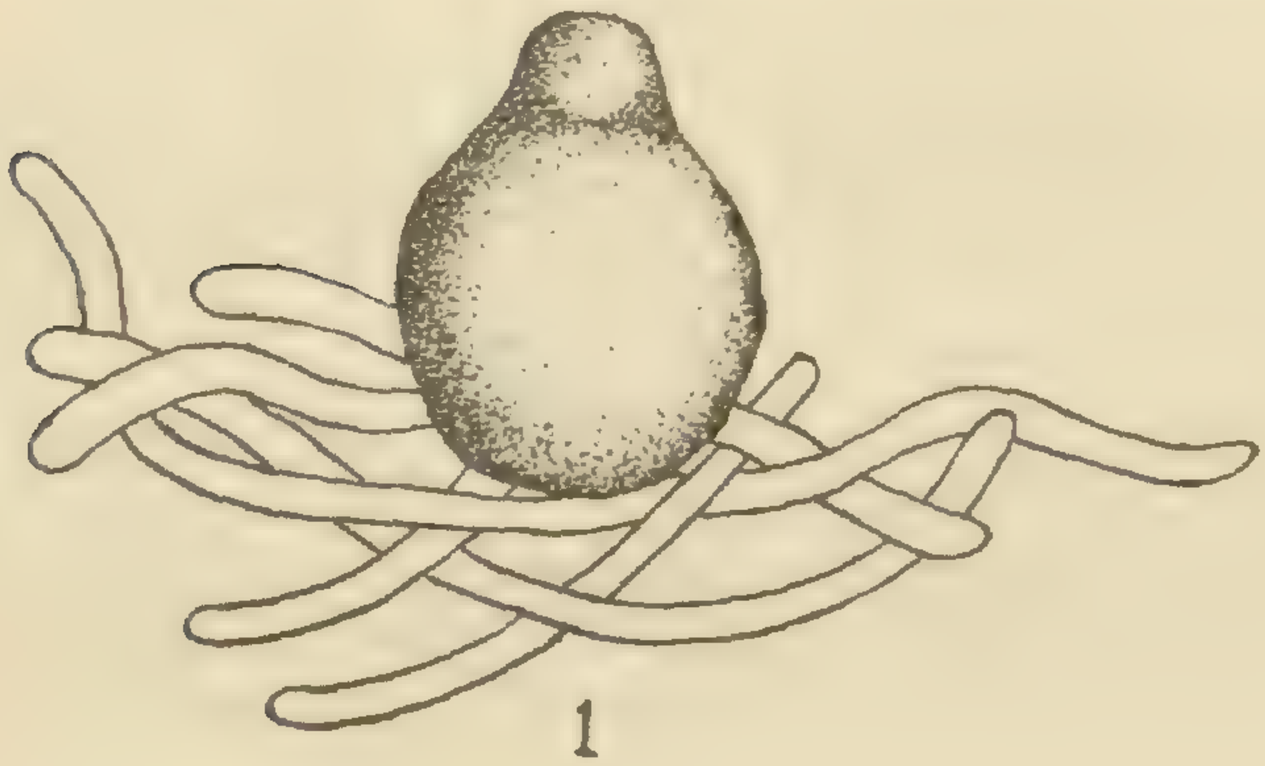
The material upon which the new genus and species of lichens here described is based was collected by Professor ROLAND THAXTER, of Harvard University, in Florida in 1897. I wish to acknowledge my indebtedness to Professor THAXTER for his kindness in placing the material at my disposal for study and description. On account of the distinctive combination of a byssine thallus and a pyrenomycetous fruit this new genus may appropriately be named as follows:

Pyrenothrix, gen. nov.—Thallus crustaceo-byssinus ecorticatus substrato arcte adnatus gelatinosus, ex hyphis tenuibus leptodermaticis crebre septatis ramosis, filamenta gonidiorum dense obducentibus. Gonidia ad species *Scytonemae* pertinentia filamentis implexis. Perithecia tenues coriacea pseudoparenchymatica, integra simplices recta nuda nigrescentia, in gonidiis sessilia nunquam immersa, ostiolis parum distinctis. Paraphyses persistentes simplices filiformes. Asci clavati. Sporae fuligineo-nigricantes murali-divisae cellulis subcubicis. Spermagonia non visa.

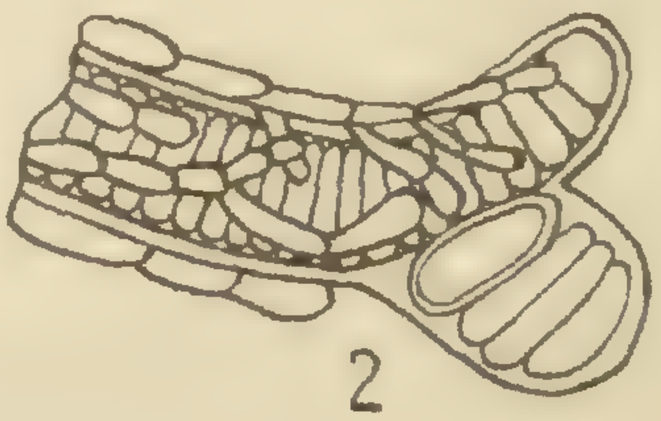
This new genus, by reason of having gonidia of the *Scytonema* type and fruit of the perithecial form (figs. 1, 2), would appear to belong most naturally to the family Pyrenidiaceae, as constituted by ZAHLBRUCKNER (ENGLER and PRANTL, Die Natürlichen Pflanzenfamilien, Teil I, Abt. 1, p. 76), but differs from all of the genera of that family hitherto described in the byssine character of the thallus (fig. 1), and in the muriform spores (fig. 4). When examined under the microscope, the structure of the thallus and the relation of hyphae and gonidia are seen to be exactly that of *Coenogonium* (fig. 2). Without entering into the much debated question, "What is a lichen?" it may be said that if *Coenogonium* is a lichen then *Pyrenothrix* is a lichen, as the two are strictly analogous. That the perithecia are not those of a secondary parasite or merely accidentally associated with the filaments of the alga is proved by the observation of early stages in their development showing their origin from the web of hyphae that envelop the gonidia (fig. 3).

Pyrenothrix nigra, sp. nov.—Thallus fusco-nigricans byssinus substrato arcte adnatus late effusus non limitatus, sicco nec flaccido nec

spongioso, madefacto molle gelatinoso, ex hyphis tenuibus (3–4 μ crassis) septatis torulosis crebre ramosis, filamenta gonidiorum crebre obducentibus; gonidiis Scytonematicis filamentis, crassitudine 13–18 μ, vaginis tenuis homogeneis non lamellosis, flexuosis implexis, rarius pseudoramosis. Perithecia minuta, altit. 200–225 μ, crassit. 160–175 μ, pyriformes collo crasso breveque, primum fuliginea demum nigrescentia, ostiolo minute parum distincto. Paraphyses persistentes simplices filiformes sat flexuosae. Asci clavatae, 8-spori. Sporae fumoso-nigricantes,



1



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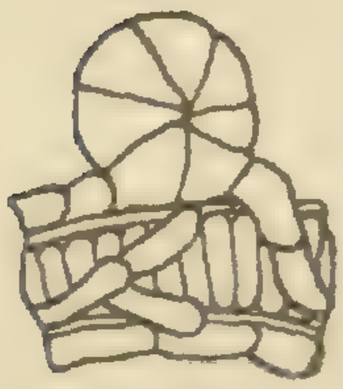

3

4

FIGS. 1–4.—Fig 1, habit sketch, ×41; Fig. 2, end of gonidial filament, showing false branch and some of enveloping hyphae (part omitted for clearness), ×385; fig. 3, early stage in formation of perithecium, ×385; fig. 4, spores, ×385.

oblongae vel late fusiformes, muriformes pauciloculares, 5–6 loculares, 2 locellati, 17–20×6–9 μ.

Thallus brownish-black, spreading over the substratum without definite limits and closely adnate, byssine, when wet soft and gelatinous, when dry harsh and not at all spongy; made up of gonidia of the *Scytonema* type, with flexuose, intertangled filaments, 13–18 μ thick, with a thin, homogeneous sheath and infrequent false branches; the filaments densely covered with septate, torulose, branched hyphae, 3–4 μ in thickness. Perithecia minute, 200–225 μ high and 160–175 μ thick, pyriform with a short, thick neck, and minute, indistinct ostiole; the wall

thin, coriaceous, pseudoparenchymatous, at first fuliginous-brown, then blackening. Paraphyses persistent, simple, filiform. Asci clavate, 8-spored. Spores smoky-black, oblong or broadly fusiform, muriform, 5–6 locular, with some of the cells once divided, 17–20×6–9 μ.

Abundant on the bark of scrub oaks at West Palm Beach, Florida, December 1897 (type!); and on living Oleander at Cocoanut Grove, Florida, November 1897; collected by Professor ROLAND THAXTER. Type specimen in the Cryptogamic Herbarium of Harvard University.—LINCOLN W. RIDDLE, *Wellesley College, Wellesley, Mass.*

CURRENT LITERATURE

MINOR NOTICES

North American flora.—The third part of Vol. 10 continues the presentation of the Agaricaceae by MURRILL,[1] the 12 genera of Pholiotanae being presented, excepting the genus *Inocybe*. The 11 genera presented include 324 species, of which 76 are described as new. The largest genera are *Gymnopilus* (85 spp.), *Naucoria* (65 spp.), *Hebeloma* (50 spp.), *Crepidotus* (46 spp.), and *Galerula* (33 spp.). The remaining 45 species are distributed among 6 genera. New species are described in *Crepidotus* (7), *Tubaria* (4), *Galerula* (8), *Naucoria* (21), *Pluteolus* (4), *Mycena* (2), *Gymnopilus* (13), and *Hebeloma* (17).—J. M. C.

NOTES FOR STUDENTS

Carbon assimilation.—JORGENSEN and STILES[2] have summarized our knowledge of the processes involved in the assimilation of carbon by green plants and the pigments concerned in them. The portion dealing with the pigments themselves has been reviewed by LINK.[3] In the introduction the reviewers express the hope that "the following pages will be of interest to those concerned in the development of scientific agriculture as well as to those interested in plant physiology for its own sake." The discussion of the path of gaseous exchange between the leaf and the surrounding atmosphere is based mainly on the work of BLACKMAN and BROWN and ESCOMBE. The conclusion reached is that the proof is now definite that the stomata are the main path of the intake of carbon dioxide into the assimilating aerial leaf of the higher plants. Any intake that may occur through the cuticle is of very minor importance. Carbon assimilation is regarded as a complex of processes which probably obey quite different laws. Attention is called to the 5 obvious factors upon which the rate of carbon assimilation in the leaf may depend: (1) carbon dioxide supply, (2) intensity of illumination, (3) temperature, (4) water supply, (5) quantity of chlorophyll. To these is added BLACKMAN'S time factor. It is found that below 25° C. the rate of carbon assimilation a little more than doubles for each rise of 10° C. For cherry laurel this gives a van't Hoff curve

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[1] MURRILL, W. A., North American flora **10**:part 3. pp. 145–226. Agaricales: Agaricaceae (pars), Agariceae (pars). New York Botanical Garden. 1917.

[2] JORGENSEN, I., and STILES, W., Carbon assimilation. A review of recent work on the pigments of the green leaf and the processes connected with them. New Phytol. reprint no. 10. London. Wesley & Son. 1917.

[3] BOT. GAZ. **62**:417–421. 1916.

in which the temperature coefficient for a rise of 10° C. is 2.1. In *Helianthus tuberosus* it was 2.5. Below 25° C. the initial rate is maintained, but above that temperature it falls off regularly. The higher the temperature the more rapid is the falling off. The falling off at any given temperature is most rapid at first and subsequently becomes less rapid.

Since it is thus impossible to measure the highest possible assimilation at high temperatures, BLACKMAN estimates it by plotting his experimental results below 25° C. (a van't Hoff curve in which $Q_{10}=2.1$) and continuing the curve by assuming that the same rule is followed above that temperature. That this curve represents the initial rate above 25° C. is confirmed in BLACKMAN'S opinion by plotting on this same diagram (the abscissae now having a time significance instead of a temperature significance) the values obtained for the assimilation rate at higher temperatures, and continuing these curves back to a point representing zero time. It is thus found that the position representing zero time for each curve is also that representing the temperature at which the readings were taken.

On this basis BLACKMAN concludes that there seems to be reason for the preliminary acceptance of the theory that the initial values of assimilation above 25° C. follow the van't Hoff curve as they do below that temperature. JORGENSEN and STILES seem disposed to defend BLACKMAN against all criticisms on this point. It must be remembered, however, that COHEN-STUART[4] has shown that, according to the van't Hoff law itself, values of Q_{10} are not constants and that the velocity is not an exponential function of the temperature. KUIJPER[5] found that such a method as BLACKMAN used on carbon assimilation did not apply to respiration. LEITSCH[6] has also found that it does not apply to temperature and rate of growth.

In regard to the light factor, the conclusion is reached that "where temperature and carbon dioxide supply are in excess the rate of assimilation is in direct proportion to the intensity of illumination." In the case of cherry laurel during the middle of an August day (temperature 29°.5 C.) the maximum assimilation was possible with 36 per cent of full sunlight, while in the case of *Helianthus* 69 per cent was necessary.

Assimilation is shown to increase directly with carbon dioxide supply until some other factor becomes the limiting one. When this point is reached, assimilation remains constant with further increases in carbon dioxide up to 0.0536 per cent. Above this point the rate of assimilation falls off rapidly. BLACKMAN'S interpretation is that this is due to the narcotic effect of the strong CO_2 on the protoplasm. The reviewers state that "BLACKMAN carefully avoids premature conclusions and tries to find non-committal expressions which will embody all his experimental results."

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[4] Konn. Akad. Wetans. Amsterdam. Proc. Sec. Sci. **14**:1159–1172. 1912.

[5] Rev. BOT. GAZ. **50**:233–234. 1910.

[6] Ann. Botany **30**:25–46.

In discussing WILLSTÄTTER'S work on the relation between chlorophyll content and assimilation rate, the reviewers state that "WILLSTÄTTER advances a simple definite hypothesis and attempts to obtain experimental data which will support his theory." WILLSTÄTTER postulates that carbon assimilation consists of two definite processes, one photochemical, taking place in the chloroplast, and one enzymatic, taking place at the boundary between the chloroplast and the plasma. The oxygen is supposedly evolved during the latter process. The experimental proof of this postulate is incomplete. The view is not a surprising one, however, since the relation of carbon assimilation and of enzymatic action to temperature both seem to be special cases of TAMMAN'S principle. The surprising thing would be that there should be only two processes concerned. The reviewers state that under certain circumstances, when no other factor is limiting, the amount of chlorophyll determines the intake of CO_2 by the leaf. WILLSTÄTTER found that the amount of pigment is not altered during the process of carbon assimilation.

The discussion of the present status of our knowledge of the known products of assimilation (oxygen and carbohydrates) is based on the work done within the last 31 years, since the earlier workers did not separate the gaseous exchanges due to assimilation from those due to respiration. It seems probable that the real assimilation coefficient (taking respiration into account) approximates unity. In considering the nature of a reaction or a series of reactions, it is very important to know the quantitative relation between initial substances and the final products of the reaction. In carbon assimilation by green leaves the relation between CO_2 taken in and O_2 evolved has not been definitely established.

The reviewers summarize in a table (p. 106) the evidence in regard to the presence of various carbohydrates in the leaf. (1) *Polysaccharides* (exclusive of cellulose and pectic substances); the presence of starch has of course long been well known, and the presence of pentosans and dextrin seems to be established. (2) *Disaccharides;* sucrose is certain, and maltose is doubtful. (3) *Hexoses;* the presence of d-glucose and d-fructose is well recognized. (4) *Pentoses;* none are positively known to be present, although there is some evidence pointing to the presence of l-arabinose and l-xylose. Definite evidence as to what sugars are absent and more quantitative data in regard to the ones present are much to be desired. The reviewers state that there is strong evidence that sugars are the first definitely known products of the assimilatory process, starch probably being a secondary product. Although most workers regard cane sugar as first, there is no satisfactory evidence that the hexoses may not be first. The mechanism of translocation is complex, depending upon differences of enzyme concentration, and possibly upon permeability changes, the nature and causes of which are at present largely unknown. The available data on energy relations are dealt with under three heads: (1) quantitative determinations of materials produced and their heats of combustion, (2) measurement of both radiant energy and heats of combustion, (3) assimilation

power of light of different wave lengths. Under (1) two methods of estimating the products of carbon are discussed: (*a*) increase in dry weight, and (*b*) amount of CO_2 taken in. The reviewers conclude that if the dry weight method can be made more accurate, it should not be lightly abandoned. If we assume with BROWN and ESCOMBE that the heat of combustion of all products of assimilation is the same as that of glucose (3.76×10^3 gram calories), we shall fall into a considerable error, as is indicated by the following values for other substances present in leaves: sucrose 3.99×10^3, starch 4.1×10^3, cellulose 4.2×10^3. If oils are present, the error in this assumption would be still greater. Actual determinations of heat of combustion made by other workers on the products of assimilation in the leaves of various plants give values varying from 4.4×10^3 to 5.2×10^3 gram calories.

Quantitative measurements of radiant energy in relation to the leaf are based on the assumption that the total radiant energy falling upon the leaf is disposed of in the following ways: (1) reflection from the leaf surface, (2) carbon assimilation, (3) transpiration, (4) transmission through the leaf, (5) thermal emission.

BROWN and ESCOMBE (1905) disregard (1) in their calculations. The reviewers believe that this is not negligible, since even a black cloth may reflect 1 per cent of the radiant energy incident upon it. PURIEWITSCH (1914) has estimated (2) in a few cases by measurement of the increased heat of combustion of the leaf per unit area. His highest value was 2.6 and his lowest 1.3 per cent. On the basis of these he calculated other cases, getting as high as 7.7 per cent. BROWN and ESCOMBE calculated (2) by assuming that one gram of absorbed CO_2 is equivalent to 0.64 gram of dry matter formed, and that the heat of combustion of the products of assimilation is 3.76×10^3 gram calories. The accuracy of these assumptions is not confirmed by measurements. Their computed values vary from 0.42 to 1.66 per cent. All of the evidence at hand thus indicates that only a very small percentage of the radiant energy received by the leaf is actually used in carbon assimilation. It might be expected that the proportion of the sun's energy used in assimilation would vary inversely as the intensity of the illumination. This expectation is not justified by the experimental data, and it is clear that we must look for some other factor on which no data are given. The reviewers point out here a case of lack of correlation of effort by investigators. If PURIEWITSCH had taken cognizance of BLACKMAN'S researches, his experiments (although regarded by PURIEWITSCH himself as preliminary) might have yielded results of much greater significance. The energy used in (3) was arrived at by BROWN and ESCOMBE by determining by weight the amount of transpiration and calculating the energy used from the heat of the vaporization of water at that particular temperature. Their results vary from 9.67 to 53.6 per cent. BROWN and ESCOMBE measured (4) directly. Their values quoted by the reviewers vary but little, the highest being 35.32 and the lowest 35.28 per cent. It is evident that (5) will usually have a positive value, since the

temperature of the leaf is usually higher than that of the air. If, however, the temperature of the leaf falls lower than that of the air, the leaf will gain energy from the air, that is, thermal emission will be negative. BROWN and ESCOMBE'S values for thermal emission are based on the same set of experiments as the data quoted under (2), (3), and (4). They are all positive. The smallest one is 6.0 and the largest is 54.60 per cent. BROWN and ESCOMBE were the first to attempt to obtain a complete balance sheet for the leaf in regard to energy. Further quantitative data correlating the work of BLACKMAN, BROWN and ESCOMBE, and PURIEWITSCH are greatly to be desired. We still have no reliable data on which any conclusion can be based as to the relative efficiency of the rays in the different portions of the spectrum.

The reviewers mention the early work, indicating that the maximum assimilation takes place in the red part of the spectrum and that there is a secondary maximum in the blue-violet end as being now of only historical interest, since the methods of measuring energy were unsatisfactory and the measurements of assimilation were crude.

The work of KNIEP and MINDER (1909), indicating that blue and red light of the same intensity produce the same assimilation and that the green light is incapable of producing assimilation, is rejected because they give no data relating to any factors other than light intensity, hence some other factor may have been a limiting one. They also reject TIMIARIZEFF'S (1903) data on the absorption of energy by chlorophyll, since he worked with alcoholic extracts, which must have contained less chlorophyll than impurities. The work of BROWN and ESCOMBE on the absorption of radiant energy by the white and the green portion of a leaf of *Negundo aceroides* is also rejected, since it is considered unfair to assume that the conditions in the green and the albino parts are the same except for the presence of chlorophyll. WEIGERT'S (1911) conclusions on the efficiency of the assimilation system are considered unreliable, since they are based on the work of BROWN and ESCOMBE just mentioned.

The reviewers introduce their discussion of theories of carbon assimilation with a sweeping condemnation of theories, making the point that those who have contributed the most valuable data on this subject have not suggested any theories. They cite DE SAUSSURE, SACHS, PFEFFER, and BLACKMAN as examples. They might possibly have added SPOEHR to the list, but they could not have added WILLSTÄTTER, since his data on the pigments of the green leaf are certainly very valuable, and considerable space is given in their review to the discussion of his theories.

Of course blind following of a theory does not lead to progress, and the desirable attitude is that of seeking for facts regardless of their bearing on any theory, but to assume that none of the workers (except SPOEHR) have been influenced by dissatisfaction with the theories that have been advanced seems unwarranted. It is not the right use of scientific imagination that is to be condemned, but the acceptance of mere imaginings as facts. JORGENSEN and STILES, of course, are quite right in their condemnation of whatever

tendency there may have been in textbooks to present BAYER'S hypothesis as representing facts.

They discuss the theories and suggestions of four men: (1) the well known theory of BAYER involving formaldehyde as an intermediate product; (2) the suggestion of VAN'T HOFF that assimilation consists of two parts, a photochemical reaction and an enzyme reaction; (3) SIEGFRIED'S suggestion that carbon dioxide may form carbamino groups with the protoplasm of the plant cell and that the photochemical reaction may then occur in a complex carbon compound; and (4) WILLSTÄTTER'S theories which, so far as they are new, are regarded by the reviewers as rather wild, the most reasonable one suggested by him being merely a repetition of SIEGFRIED'S suggestion.

In the end it appears that we have at present no satisfactory theory of the changes that take place between the entrance of CO_2 into the plant and the production of carbohydrates.

Although deploring the lack of coordination among the various workers, and the tendency of botanists to accept without question the suggestions of physicists and chemists as to the nature of plant processes, the reviewers conclude that plant physiology is developing into an exact science, utilizing the experiences of the fundamental sciences, physics and chemistry, but having working principles and methods of its own. That it will thus be of great service in plant production requires no prophetic vision.—GEORGE B. RIGG.

Studies on oxidases.—In connection with his work on plant oxidases, BUNZELL[7] has published results of an investigation of the effect of hydrogen-ion concentration, C_h, on oxidase activity. Using his own simplified oxidase apparatus to measure oxidation and the gas chain to measure hydrogen-ion concentration, he finds that the oxidase activity of several kinds of material from potato tubers is completely inhibited by a C_h of $2.0–2.8 \times 10^{-4}$. The various concentrations were obtained by adding sodium hydroxide and acetic acid in various proportions, or either one alone, to mixtures of the plant material and pyrocatechin.

It is worth noting here that the two together constitute a true buffer solution capable of maintaining a fairly constant hydrogen-ion concentration, but that neither one alone suffices. Consequently, if there is a tendency for the acidity to increase in the Bunzell apparatus, as suggested by ROSE[8] in 1915, conditions are not comparable in the different mixtures. Those containing the true buffer solution will have practically a constant C_h throughout the course of the experiment, while those containing only sodium hydroxide or acetic acid will have a C_h which is larger at the end than at the beginning. The

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[7] BUNZELL, H. H., The relationship existing between the oxidase activity of plant juices and their hydrogen-ion concentration, with a note on the cause of oxidase activity in plant tissue. Jour. Biol. Chem. **28**:315–333. 1916.

[8] ROSE, D. H., Oxidation in healthy and diseased apple bark. BOT. GAZ. **60**: 55–65. 1915.

latter condition holds true also for the controls, containing only water, pyrocatechin, and plant material. Furthermore, if the C_h changes during the experiment and only the initial concentration is determined, as in BUNZELL'S work, no very accurate conclusion can be drawn as to the effect of this factor on oxidase activity.

BUNZELL finds the inhibiting concentration for tulip tree material to lie between 1.58 and 5.02×10^{-3}, and for the magnolia between 3.5×10^{-3} and 8.91×10^{-4}. He considers that his results show "that the acid sensitiveness figure is a rather fixed number for any particular genus." He says also that it even seems "that the acid sensitiveness constant is the same or nearly the same for different genera (tulip and magnolia) of the same family (Magnoliaceae)." An analysis of his table III shows in general that the less the natural acidity of the plant material the lower the C_h necessary to cause total inhibition of its oxidase activity. This relation does not seem to hold in all cases, possibly because the various degrees of acidity used were too far apart to establish the inhibiting concentration with any great degree of accuracy.

If further work should prove such a relation general, new force will be added to the suggestions of BUNZELL and others that there is a distinct oxidase for each plant or group of closely related plants; not necessarily because they are protein in nature, however, as BUNZELL supposes. They may resemble each other in plants of the same family; they may show various properties of proteins, such as denaturing by acids, alcohol, and heat, and still be something quite different from proteins. BAYLISS suggests, on the basis of work by BACH and CHODAT and others, that oxidases are merely some form of iron copper or manganese kept in a disperse condition by various colloids. If these colloids are proteins the action of acids, for example, removes them as dispersing agents and allows the oxidases to precipitate. As a result of absorption, the two may come down together as a single precipitate which gives both protein and oxidase reactions without ever having existed as a real compound in the living plant. Such a hypothesis, however, fails to apply to peroxidases, for these, according to BEHRING, ASO, and BACH and CHODAT, are very little affected by heat. BACH and CHODAT also found that horseradish peroxidase when carefully purified contains no iron or manganese.

In connection with BUNZELL'S "acid sensitiveness figure," the question arises whether the inhibition he noted was all due to acidity. When a buffer solution of any sort is used to establish a definite hydrogen-ion concentration, elements are added which in the quantity used may be entirely foreign to the plant and productive of anomalous results. Illustrations of this are seen in BUNZELL'S table III. For example, extract of potato peeling with a natural C_h of 1.02×10^{-6} (no buffer solution being present) caused 22 per cent more oxidation than the same extract when a buffer solution was present and the C_h practically the same (1.04×10^{-6}). Even more marked are the results with potato sprouts, for with the C_h just about the same whether the buffer solution were present or not, they gave 16 per cent more oxidation without

it than with it. The data presented for "tulip tree leaves 1915" and "scaled tulip tree buds" show that when the solution in the oxidase apparatus had the natural reaction of the plant material, the oxidations were respectively 6.6 and 12 per cent greater than when the C_h, established by a buffer solution, was actually less than the natural C_h. In such a case it seems evident that some factor other than the hydrogen-ion concentration was effective as an inhibitor. The possibility that other ions play a part is indicated by work now being carried on by KRAYBILL and the writer.

The paper concludes with a brief review of the evidence, obtained by BUNZELL and others, of an increased oxidase activity in the leaf tissue in the case of physiological disturbances, and the possible meaning of such an increase. No mention, however, is made of work by ROSE on healthy and diseased apple bark in which it was shown that there is a much greater oxidase activity in the latter, correlated with a lower hydrogen-ion concentration.

REED,[9] in a paper published about the same time as BUNZELL'S, puts the inhibiting C_h for oxidase of potato extract at 5.5×10^{-4} (slightly higher than the $2.0-2.8\times10^{-4}$ found by BUNZELL), and for that of Red Astrachan apples at $5.0-7.0\times10^{-4}$. His statement that these concentrations are much lower than those given by previous investigators fails, however, to take account of BERTRAND'S report[10] in 1907, that a n/5000 solution of sulphuric acid ($C_h = 5\times10^{-4}$) completely inhibited oxidation by sap of the lac tree. REED'S results would have meant more if he had measured oxidation by the BUNZELL apparatus rather than by the relatively inaccurate method of noting color changes, even though the BUNZELL apparatus, because of the poorly understood effects of hydrogen-ion and other inhibitors, leaves much to be desired in the way of accuracy.

One point is well made in this paper, namely, that plant extracts have an acid absorbing power which must cause inaccuracy in interpreting results obtained by adding buffer solutions to them if such results are not checked by careful determinations of the hydrogen-ion concentration. He found that when a given volume of 0.01 molar HCl was added to an equal volume of potato extract, the hydrogen-ion concentration, which should have been 5×10^{-3} if the potato extract acted like water, was actually only 5×10^{-4}. This decrease in acidity he thinks is due to proteins present in the extract as well as other amphoteric electrolytes, including probably phosphates and carbonates.

It is unfortunate, to say the least, that the authors of these papers have failed to cite adequately the literature pertinent to the phase of the subject with which they are dealing. Each has made a definite contribution to our

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[9] REED, G. B., The relation of oxidase reactions to changes in hydrogen-ion concentration. Jour. Biol. Chem. 27:299–303. 1916.

[10] BERTRAND, G., Bull Soc. Chim. France 1:1120. 1907.

knowledge of the factors affecting oxidase activity, but the true value of this contribution would have been better shown by a fuller reference to other work.

KASTLE and BUCKNER[11] report experimental proof that phenolphthalein can be oxidized in the living plant. This they take to mean that free active oxygen is present in the tissues, apparently overlooking the possibility that combined oxygen might have caused the results observed. The reagent used, on oxidation, yields phenolphthalein, which is easily recognized by the pink color it gives with alkalies. When this test was applied to stalks of Indian corn which had been injected with the reagent, the pink color was found localized in the fibrovascular bundles of the stem and leaves. It was not found in the tassel, although lower down, close to the point of injection, there had been some diffusion into the cells adjoining the fibrovascular bundles. Similar results as to place of oxidation were obtained with okra.

The method here used offers a means of attacking the problem of oxidation in plants which should yield other valuable results if further developed and applied to a wider series of plants. It would be worth while to try whether phenolphthalein can be oxidized in the living plant when used in neutral or acid solution, and if so whether the oxidation is localized in particular cells or tissues. Such a test would allow for the effect of reaction (acidity or alkalinity), a factor known to be of great importance, not only in oxidation processes, but also in other processes carried on in living tissues. The effect of reaction might also be studied in acid fruits and in tissues affected by "physiological diseases" or by diseases due to bacterial or fungus parasites. In several cases such tissues have been found to be less acid than healthy ones, but little is known concerning variations in reaction within the tissues themselves.—D. H. ROSE.

Experiments in girdling.—A contribution by HIBINO[12] is of interest both to plant physiologists and horticulturists, since it will aid in furnishing a more definite chemical basis for the interpretation of the behavior of girdled plants. In the past there has been no lack of references to the accumulation of elaborated foods above the girdles; it is certainly worth while to have some definite determinations of these compounds and their relative quantities.

Five types of girdling were tried on *Cornus contraversa* Hemsl. These consisted in (1) removing a complete ring of bark, (2) removing a complete ring of bark and some of the wood, (3) removing half a ring of bark, (4) removing half a ring of bark and wood, and (5) boring completely through the wood. The wounds were left unprotected. The last three methods of treating the material resulted in responses similar to the untreated controls in nearly all cases.

The general external results noted are those commonly recorded in girdling experiments. The main interest of the present paper centers in the presenta-

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[11] KASTLE, J. H., and BUCKNER, G. DAVIS, Evidence of the action of oxidases within the living plant. Jour. Amer. Chem. Soc. **39**:479–482. 1916.

[12] HIBINO, SHIN-ICHI, Effekt der Ringelung auf die Stoffwanderung bei *Cornus controversa* Hemsl. Jour. Coll. Sci. Imp. Univ. Tokyo **39**:1–40. *pls. 1, 2.* 1917.

tion of material which may aid in an explanation of the cause of these conditions. Unfortunately the experiments are limited and the analyses of the nitrogenous compounds are not sufficiently complete to furnish any sort of basis for judging what rôle they may play. The data on the carbohydrates, however, are of considerable interest. In studying the effects of girdling on nutrition in general, at least three of the many points concerned in growth must be considered: (1) a possible modification of the intake of nutrients by the roots; (2) the synthesis of products from these compounds and those resulting from photosynthetic activity; and (3) whether these compounds are stored or utilized. We are given some light on the third point only. It is a fair question to ask whether the ability of the roots to take up salts is not as profoundly modified by the character and quantity of the organic nutrients in the parts above ground and with which such salts may be combined, as it is by the so-called starvation effects brought about by cutting off the supply of organic nutrients from the tops to the roots. Girdling could bring about both of these situations. The question arises as to why the carbohydrates accumulate above the girdles. As commonly stated, this may be due to the fact that these products are held from passing into the roots. There is little evidence which would show that it may not also be due to a deficiency of mineral nutrients, particularly nitrates, to aid in their utilization in forming other compounds or growth. A study of the ratios of carbohydrates to moisture, nitrogenous compounds, and other mineral nutrients in their relation to the entire phenomenon of growth is greatly to be desired. While this situation is not dealt with by HIBINO, his results and those of several previous investigators furnish ample encouragement to warrant investigation.

The increase in anthocyanin accompanying an increase in reducing sugar confirms the findings of previous workers with other plants. The yellowing of the foliage above a girdle is a usual condition. That this should accompany an increase in carbohydrates is interesting. It is unfortunate that no analyses of the nitrogenous compounds in the leaves are available. Lacking such determinations nothing can be said concerning their possible relationship to the carbohydrate situation, nor the moisture situation. The fact that the percentage of moisture in the leaves is lower when carbohydrates form a higher percentage of the weight might be expected when the moisture holding capacity of these compounds is considered.

The single quantitative determination of the reserve materials in the twigs in midwinter is not sufficient for any general conclusions. Again, it is unfortunate that all the nitrogen is computed as protein. It is more than likely that all of it is not, and quite probable that the several forms of nitrogen may exist in different proportions in the several lots examined. A quantitative analysis at the time of active vegetation would have been even more significant regarding the influence of the several substances on growth. Striking as are the differences in the several lots, the results cannot be interpreted with certainty unless compared with figures for similar parts at several periods during the

year. Whether the differences shown by the bark and wood girdled material may be accounted for by a decreased moisture supply in the latter is an open question. It is interesting to note, however, that many plants grown with a deficiency of water do show an increased tannin content.

While it is impossible to draw broad conclusions from the results presented, the work constitutes a genuine contribution toward a more nearly complete knowledge of the causes of the responses following girdling, and adds to the available information on the entire problem of growth. In any future work it would be particularly desirable to follow the nitrogenous compounds and mineral nutrients as well as the carbohydrates, more especially with a view toward the determination of the ratios of these various substances in relation to the observed responses.—E. J. KRAUS.

Imbibition.—MACDOUGAL[13] and MACDOUGAL and SPOEHR[14] are doing work on the effects of acids and bases on imbibition of water by plant tissues and plant gels that promises to be the most significant contribution in this phase of plant physiology that has been made for some decades. Practically all of the work on the effect of acids and bases on the amount of swelling and force of swelling of gels and on the viscosity and osmotic pressure of sols has been done on the amphoteric protein gels. For these it seems well established that the iso-electric point (the reaction at which the particles are without a charge) is the point of minimum swelling, force of swelling, osmotic pressure, and viscosity, and that forcing the ionization of the gel or sol either to the positive by addition of an acid or to the negative by the addition of a base increases the swelling, osmotic pressure, and viscosity very markedly.[15]

MACDOUGAL and SPOEHR find that both base and acid additions (n 0.01) decrease greatly the swelling of agar plates and to a less degree of *Opuntia* tissue. In fact, *Opuntia* tissue acts more like mixtures of gelatine and agar than it does like either gelatine or agar. These results suggest that in contrast to the protein gels and sols, the point of maximum swelling, viscosity, etc., in agar is the iso-electric point and that the positive agar due to acid addition or the negative agar due to base addition shows a lowering of these characters. In this connection it is to be regretted that the H^+ concentration for the iso-electric point of agar has not been determined. It is also desirable to know the behavior of various other carbohydrate gels and sols (mucilages, pectic materials, gums, etc.) to see whether this contrast in behavior is a general difference between the protein and carbohydrate gels. It seems that plant physiologists have generally assumed that the laws of behavior of protein

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[13] MACDOUGAL, D. T., Imbibitional swelling of plants and colloidal mixtures. Science **44**:502–505. 1916.

[14] MACDOUGAL, D. T., and SPOEHR, H. A., The behavior of certain gels useful in the interpretation of the action of plants. Science **45**:484–488. 1917.

[15] HOBER, R., Physik. Chemie Zelle Gewebe. 329–338. 1914.

colloids hold for all hydrophilous colloids with which they have to deal, protein as well as carbohydrate. This work seems to make evident the error of such a general assumption.

A quotation from the last paper gives the author's view of the physiological significance of these results. "The general identity of constitution of these colloidal mixtures and of cell-masses, and the obvious similarity of their behavior, together with newly determined features of carbohydrate metabolism not described in this paper, make it possible to correlate more closely the processes of imbibition, metabolism, and growth, and on the bases of these interrelations, to interpret growth enlargement and incidental variations in volume and size of organs." No doubt many will differ from a statement in another part of the paper that amorphous carbohydrates form a very important part of the plant protoplast. There seems little evidence that amorphous carbohydrates (excepting starch, which would have no bearing here) are general constituents of the plant protoplast. When amorphous carbohydrates are constituents of the protoplast they generally appear as discrete particles of micronic size and not in intimate mixtures with proteins and distributed in particles of submicronic or amicronic size, as must have been the case in the agar gelatine mixtures with which the authors worked. Of late we are coming to know that amorphous carbohydrates of the walls and intercellular spaces have considerable physiological controlling action. This is especially true in seeds. This work is very suggestive in this connection also.

This work may have a very important bearing on the daily transpiring power of certain of the cacti as found by various workers in the Desert Laboratory. In these there is apparently no stomatal regulation, and the lowest transpiring power is during the day. This corresponds to the daily change in acidity. The time of low transpiring power is the time of low acidity, when, according to the findings of MacDougal and Spoehr, the gels of the tissues will have the greatest power to take up and hold water. With this no doubt there will be a rise in viscosity. These physical conditions will all tend to lower the rate of movement of water toward the intercellular spaces and to lower the vapor pressure within those spaces. This in turn will lower the rate of outward diffusion. This suggested relation needs careful investigation. On the basis of the behavior of protein gels the daily variation in the transpiring power of the cacti was not intelligible. This work should be a great stimulus to much work along similar lines.—Wm. Crocker.

Taxonomic notes.—Britton,[16] in continuing his studies of West Indian plants, has described new species in *Cleome*, *Chamaecrista* (3), *Leucocroton* (3), *Passiflora* (3), *Rondeletia* (10), *Eriocaulon* (3), *Dupatya*, *Pilea*, *Ichthyomethia*,

[16] Britton, N. L., Studies of West Indian plants. IX. Bull. Torr. Bot. Club 44:1–37. 1917.

Castelaria, and *Stenostomum* (2). There is a synopsis of the species of *Chamaecrista* in the West Indies (31 spp.); of the Cuban genus *Leucocroton* (7 spp.); of *Passiflora* in Cuba (21 spp.); and of *Rondeletia* in Cuba (35 spp.).

DECANDOLLE,[17] in a study of specimens of Meliaceae from Central America and Panama sent by the United States National Museum, has described 9 new species in *Guarea* and 2 in *Trichilia*.

HEDGCOCK and HUNT[18] have described 5 new species of *Peridermium* on pine needles in the eastern United States.

KERN,[19] in a monograph of the North American "sedge rusts," recognizes 19 species of *Puccinia*, 3 of which are described as new.

PENNELL,[20] in continuing his studies of our southern plants, has presented the genus *Chamaecrista* as represented in the United States. He recognizes 13 species, which include 3 new species and 2 new combinations.

WAGER[21] has published a list of the mosses of South Africa, which for the first time brings together all the known mosses of South Africa. The list includes 846 species in 160 genera, representing 37 families. The names of 27 new species, representing 23 genera, are also included, one of the genera (*Physcomitrellopsis*) being new. These will be described and published later.

WILLIAMS,[22] in reporting the mosses obtained on a collecting trip in the Philippine Islands, extending from October 1903 to August 1905, lists 240 species in 118 genera. Of these, 27 species and 3 genera (*Rhabdoweisiella*, *Pseudopohlia*, *Stereodontopsis*) are described as new.—J. M. C.

Endosperm color in maize.—In crosses between California Golden Pop maize and a white endosperm variety obtained from HAAGE and SCHMIDT under the name *Zea Caragua*, WHITE[23] finds white dominant. These results are interpreted by assuming the presence of an endosperm suppression factor *A* in the *Zea Caragua* in addition to the usual color factor *y*. , This new primary factor affecting endosperm color raises the number of such factors to three; in addition there are numerous secondary factors.—E. M. EAST.

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[17] DECANDOLLE, C., Meliaceae Centrali-Americanae et Panamenses. Smithson. Miscell. Coll. **68**:no. 6. pp. 8. 1917.

[18] HEDGCOCK, GEO. G., and HUNT, N. REX, New species of *Peridermium*. Mycologia **9**:239–242. 1917.

[19] KERN, FRANK D., North American species of *Puccinia* on *Carex*. Mycologia **9**:205–238. 1917.

[20] PENNELL, FRANCIS W., Notes on plants of the southern United States. III. Bull. Torr. Bota Club **44**:337–362. 1917.

[21] WAGER, H. A., A check list of the mosses of South Africa. Publ. Transvaal Museum, Pretoria. pp. 20. 1917.

[22] WILLIAMS, ROBERT S., Philippine mosses. Bull N.Y. Bot. Garden **8**:331–378. *pls. 171–174.* 1917.

[23] WHITE, ORLAND E., Inheritance of endosperm color in maize. Amer. Jour. Botany **4**:396–406. 1917.

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